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MULE DEER
IN THE MISSOURI RIVER BREAKS, MONTANA

A Study of Population Dynamics in a Fluctuating Environment

Kenneth L. Hamlin
Richard J. Mackie

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FINAL REPORT

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Ken Hamlin and Dick Mackie

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CHAPTER 1

INTRODUCTION AND PERSPECTIVE

Mule deer (*Odocoileus hemionus*) are the most widely distributed and abundant of all species of large mammals native to western North America. Important populations occur throughout a broad spectrum of habitats or environments--from relatively moist and dense coniferous forests to dry, open plains and deserts. The quality of these habitats for deer varies greatly as a result of broad differences in physical and biotic characteristics. Many are highly variable environments in which habitat quality also fluctuates seasonally and annually due to variation in weather conditions. Mule deer habitat relationships and population characteristics and dynamics, as well as management opportunities and constraints vary accordingly. However, long-term studies addressing spatial and temporal differences in population ecology and their significance in management are lacking.

Our studies of mule deer in the Missouri River Breaks of northcentral Montana have provided a 28-year data set on ecology and behavior of the species in a representative, historically important and environmentally variable habitat. The studies began with investigation of range ecology and relationships of mule deer, elk, and cattle on the area during 1960-1964 (Mackie 1965, 1970). This provided basis and methodology for continuing population surveys to determine mule deer population characteristics and trends in relation to range conditions through the early 1970s (Mackie 1973). A marked decline in mule deer populations and low fawn recruitment despite seemingly favorable range conditions during 1973-1975 brought support for intensive studies of population ecology and factors regulating deer populations on the area during 1975-1987.

Our first priority was to provide knowledge for management of mule deer in "breaks" habitat. However, the results also may be important from a more theoretical point of view. Few, if any, serious ecologists would deny that existing knowledge of population ecology has many shortcomings. Despite myriad theoretical, experimental, and field studies, questions and confusion about pattern and process in population organization, population-habitat relationships, and population dynamics and regulation persist. Reasonably accurate long-term data on population ecology of deer and other large mammals are rare. Thus, Caughley (1980) notes that, aside from McCullough's (1979) study of white-tailed deer in the George Reserve, Sinclair's (1977) study of African Buffalo, the long-term studies of moose and wolves on Isle Royale, and the work of Laws and his associates

on elephants in east Africa, "most of the other studies that have been done coalesce into an amorphous mass of nothing much."

We believe our data set is sufficiently complete and accurate to show not only what the mule deer population has done, but why, and to address broader questions relating to issues such as carrying capacity, population regulation, yield theory, predation, and habitat selection. Perhaps somewhat more specifically, we can also address the extent to which "...the principles derived [from studies of white-tailed deer on the Edwin S. George Reserve in southeastern Michigan] are general and should apply to most large, long-lived mammals--in modern ecological parlance, K-selected species" (McCullough 1979).

We also attempted to answer age-old questions about population regulation. What determines the size of a population? Why do certain numbers occur at one time and place and other numbers at different times and places? The mule deer population we studied did not increase without limit nor did it decline to extinction. Yet, population regulation in its traditional sense is not a proper phrase for the dynamics we observed. Our results and conclusions concern population ecology and all its attendant interrelationships. The total environment of the population and its inherent heterogeneity and dynamics must be considered to understand population dynamics. We concur with Ratcliffe (1958) that animals in a population cannot be regarded simply as 1/N. Individual differences in animals and the heterogeneity of their common and individual environment in time and space are all important elements of population ecology and "regulation".

General Theories of Population Regulation

Ecological literature of the last 50 years is replete with books and articles by proponents of various theories of population regulation. These include many syntheses, reinterpretations, and reviews (e.g. Milne 1957, Krebs 1972, and Murray 1979). Because no one theory or school of thought has been universally accepted as yet, a brief review of previous and current theories of population regulation, generally and among ungulates, is necessary to place our study and conclusions in perspective.

The primary problem or question related to population dynamics and regulation that theorists and empiricists have tried to answer is composed of 2 parts. Krebs (1972: p. 269) pointed this out when he stated: "One can make two fundamental observations about populations of any plant or animal. The first is that abundance varies from place to place . . . The second observation is that no population goes

on increasing without limit, and the problem is to find out what prevents unlimited increase in low-and high-density populations. This is the problem of explaining fluctuations in numbers."

The observation that no population increases without limit and that substantial destructive or debilitating forces were necessary to hold numbers in check was apparently the original impetus behind the study of population regulation. Malthus (as quoted by Davis 1950) believed that the ultimate check was food, but the immediate check was "all those customs and diseases generated by a scarcity of the means of subsistence". Darwin (1872: p. 54) observed: "There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair." Although the works of Malthus and Darwin inspired the search for methods of population regulation, most existing theories were framed by the work of entomologists and a few fisheries scientists from the early 1900s through the 1950s.

Existing theory about pattern and process of population regulation has generally developed around 4 schools of thought. One of the earliest and, in some form, perhaps that most widely held today, is often called the biotic school. Although most commonly associated with Nicholson (1933), Howard and Fiske (1911) had earlier promoted much the same views. Nicholson believed that there was a balance in nature. In order to achieve a state of balance, he stated it was essential that a controlling factor should act more severely at high densities and less severely at low densities. He suggested that the chief "density-dependent" factor controlling population level was intraspecific competition for resources. Mathematical expression of this theory was accomplished (Nicholson and Bailey 1935), but its assumptions about the animals (1/N) and especially the environment (constant) were viewed as unnatural by some (Milne 1957).

A second school of thought developing during the same period was that weather or climate was responsible for control of populations (Uvarov 1931). Nicholson attempted to define this school out of existence by stating that, because climate was not affected by population density, it could not be a controlling factor. He was really saying that weather couldn't be a controlling factor because it did not meet *his* assumption that *only* factors affected by population density could control populations. Apparently, the possibility that the effect of weather can vary with density was not considered important. The density-dependent school of thought already was so entrenched that the circular reasoning behind ruling weather out as a controlling factor aroused little comment.

A "comprehensive" school of population regulation also developed (Thompson 1929, Andrewartha and Birch 1954). Theories developed therein held that at some time, all factors were involved in population control. In contrast to the "balance" emphasized by Nicholson, these authors emphasized the constant fluctuations of populations and indicated that populations were controlled by the total environment. The importance of weather or climate as a major regulating factor is usually apparent in the models of this "school" (Birch 1957). Milne (1957: p. 260) summarized the view of Thompson as follows: "where and when the organism meets favorable conditions its numbers increase, but these conditions never endure long enough for unlimited increase; nor do unfavorable conditions endure long enough for a decrease of numbers to zero--except in places that are in any case unsuitable for the organism." This view was essentially the same as that of Andrewartha and Birch (1954) in that the most important way in which animal populations are limited is "by shortage of time when the rate of increase, r, is positive." Milne's (1957: p. 265) own theory generally agreed with the comprehensive school, though he revived density related terms: "For the most part, control of increase is due to the combined action of (a) density-independent and (b) imperfectly density-dependent environmental factors." Milne believed that only rarely did the perfectly density-dependent factor of intraspecific competition play a role in population control. He also believed that a balance occurred in the environment, not between populations and the environment; that is, over time and space, favorable environmental conditions were balanced by unfavorable environmental conditions. A more recent comprehensive view (Huffaker and Messenger 1964) held that density-dependent processes control populations in favorable environments and density-independent factors control populations in unstable or marginal habitats.

These earliest theories centered on the role of extrinsic factors in population regulation: food, predators, weather, disease, shelter, etc. (Krebs 1972). Intrinsic factors and individual differences in animals were largely ignored. They came to the fore, however in a new school of thought, developed in the mid- to late- 1950s, which emphasized individual differences in animals and proposed that intrinsic changes in the population could lead to *self-regulation* (Chitty 1955, 1960).

Proponents of self regulation believed that uncontrolled competition for resources could ultimately lead to destruction of the food base and extinction. Because most populations do not decline to extinction, it was argued that some form of self regulation must hold animal population levels below those where resource destruction occurs.

Natural selection among individuals and evolutionary changes in a population are important concepts in self regulation theories. As population numbers rise during favorable periods, more individuals of "lower quality" or viability survive. Thus, the effect of weather can be "density-dependent", being more severe at high populations with more "low quality" individuals.

Because the genetic composition of a population can vary over time and with conditions, the "self-regulation" process could work through a genetic feedback mechanism (Pimentel 1961). Variations on the intrinsic (self-regulation) school of thought include the effects of: 1.) behavior, e.g. territoriality (Wynne-Edwards 1965); 2.) physiological change resulting from stress at high densities (Christian and Davis 1964); and 3.) the Chitty Hypothesis (Chitty 1967, Krebs 1978) that population regulation can result from genetic-based changes in spacing behavior.

Although theories and variations of theories on population regulation have come and gone, most widely held views include the major theses of Nicholson (1933) and Smith (1935). These imply a "balance of nature" and that factors controlling populations, whether intrinsic or extrinsic, act in a density-dependent manner.

Population Regulation in Ungulates

Until recently, most theoretical and empirical work on population dynamics and regulation was confined to insects, fish, small mammals, and to some extent birds. However, the major "principles" derived were believed general and applied in practice to ungulates. It was only during the mid-to-late 1970s that results of long-term studies on large mammals began to appear (Laws et al. 1975, Sinclair 1977, Peterson 1977, McCullough 1979, Botkin et al. 1981). Although these studies have raised many questions and stimulated discussion, they have not resulted in major new theories of population regulation.

Peek (1980) summarized current thinking on natural regulation of ungulates as reflecting 1 of 2 perspectives; an ungulate-habitat interaction and a predator-ungulate interaction. The ungulate-habitat interaction model is most widely held and applied. It is essentially Nicholsonian in that density-dependent intraspecific competition for resources is the main regulating factor. Especially for North American deer (Davis 1950, Lack 1954, Dasmann 1971), this came to mean that they were forage-limited. It was long believed that deer were not territorial (Smith 1976, Coblentz 1977, Peek 1980), nor did they have any other intrinsic mechanisms of control. Thus, in the absence of predators, they were inherently

irruptive, overused their forage resources, and temporarily or permanently reduced the carrying capacity (K) of their range. Caughley (1976a, 1979) modified this somewhat by indicating that generally an equilibrium population results from the dynamics of ungulates interacting with the dynamics of the plants on which they feed. Populations of both herbivores and plants fluctuate and each affects the other. Ungulates are the major or only factor affecting forage production in these models, at least in the way they are generally presented.

For wildlife managers, the concept of deer irrupting, exceeding their forage base, and then abruptly declining to lower levels probably has its roots in the Kaibab deer incident (Rasmussen 1941). In textbooks and classrooms, the Kaibab story is the "classic" example used to indicate that, at least in the absence of predators, deer will "overuse" their forage and reduce carrying capacity. Interpretations have varied in their emphasis on the importance of predation and interspecific competition (livestock grazing) in the process, but the Kaibab story has generally been viewed as a typical example of intraspecific competition and delayed density-dependent mortality (Lack 1954). More recently, Caughley (1970) questioned the reliability of the data on the Kaibab deer herd and Burk (1973) termed the Kaibab incident "a myth."

The predator-ungulate interaction theory of ungulate population regulation (Peek 1980) was supported by indications that most irruptions of ungulates took place in the absence of predators. This theory holds that, in the presence of predators, herbivore populations seldom approach limits imposed by food. Hairston et al. (1960) and Slobodkin et al. (1967) provided a theoretical framework arguing that predation regulates the dominant members of the herbivore trophic level. Recent work (Bergerud 1971, Keith 1974, Beasom 1974, Bergerud 1978, Stout 1982, and Gasaway et al. 1983) indicated that, at least in some circumstances, predation can have a significant impact on ungulate population dynamics. According to Gasaway et al. (1983): "One of the most significant lessons to be learned from the patterns observed in Minnesota, Alaska, and on Isle Royale is that a combination of controlling factors can initiate a decline in ungulates, which may then continue to very low densities as wolf predation becomes an increasingly important controlling factor."

The predator-ungulate interaction model is basically a modification of the ungulate-habitat interaction model, and most adherents of the former seem to believe that in the absence of predators, the latter is applicable. There are also those, however, who believe the predators cannot regulate populations even when they are present and abundant; thus, the ungulate-habitat interaction model is always applicable.

Multiple equilibrium models (Haber 1977) combine the 2 other models and hold that predators are important at low ungulate densities but that at high densities, ungulates escape the influence of predators and are influenced by density-dependent intraspecific competition for resources.

Because density-dependent intraspecific competition for resources has been assumed to be major factor regulating ungulate populations, human predation (hunting) is often neglected in studies of factors controlling populations. Management theory usually assumes that hunting losses are compensated for by decreased mortality and increased reproduction and recruitment of young among survivors.

Recently, some authors (Geist 1981, Ozoga et al. 1982) have suggested that behavior may be more important than previously realized in determining deer population size, structure, and dynamics. However, these views have subsequently received little attention or comment by others.

The Concept of Carrying Capacity

Because most applied management theory for ungulates is based on the ungulate-habitat interaction model, a discussion of population ecology and regulation necessarily includes discussion of the carrying capacity concept.

In general, "carrying capacity" refers to the number or density of animals a given habitat/environment can support. A good review of the concept, its use, and interpretation is provided by Macnab (1985). The terminology and components included in specific definitions vary widely, but animal-vegetation (forage) interactions similar to those underlying range-domestic livestock relationships and livestock production pervade most interpretations applied to deer and other wild ungulates. Thus, Macnab (1985) notes "For range management, the density of cattle providing maximum sustained production of beef is the carrying capacity of the land." More generally, Caughley (1979) states "Carrying capacity is the name we give to an equilibrium between animals and vegetation, and we index the position of that equilibrium by its characteristic density of animals." Such definitions would also indicate or at least imply that carrying capacity is a more or less finite entity, varying only in relation to changes in vegetation/forage supplies induced by animal-plant interactions.

Alternatively, some theoretical definitions have recognized that "carrying capacity" may be determined by many factors and may vary considerably. Foote (1971), for example, defined carrying capacity as "The sum of the environmental factors which make a game range habitable," and further stated

that "Carrying capacity changes from season to season on the same range." This complexity and the variable nature of carrying capacity was also pointed out by Edwards and Fowle (1955) when they stated: "The really important thing is to recognize that carrying capacity is not a stable property of a unit of environment but the expression of the interaction of the organisms concerned and their environment. Moreover, the carrying capacity of an ecosystem may fluctuate in response to the ebb and flow of interactions going on within it." Sinclair (1981) similarly noted "A population at carrying capacity should not be thought of as one with a stable or constant level. Rather, it is one that is fluctuating, often extensively, between certain boundaries." Hobbs et al. (1982) have empirically shown extensive annual fluctuations in energy-and nitrogen-based estimates of carrying capacity for elk (*Cervus elaphus nelsoni*) winter range.

Following the concept that carrying capacity reflects the availability of forage resources and forage-animal interactions, different definitions and terminology have been proposed or applied, based on the management objectives for a given population. The maximum or equilibrium number of animals that can be supported under natural conditions (in a non-hunted area) has been variously termed subsistence density (Dasmann 1981), environmental carrying capacity (Clark 1976), K carrying capacity (McCullough 1979), potential carrying capacity (Riney 1982), and ecological carrying capacity (Caughley 1979). By definition, the rate of increase of both plants and herbivores at K carrying capacity is zero (Macnab 1985). "Equilibrium" is reached through a sequence of increased juvenile mortality, increased age of sexual maturity, decreased birth rate among adults, and increased adult mortality (Macnab 1985).

For managed populations in which harvesting occurs, following the concept of maximum sustained yield (MSY), other definitions and terminology have been proposed and applied to "carrying capacity." This position on the continuum of possible ungulate/vegetation densities (Macnab 1985) has been called optimum density (Dasmann 1981), "I" carrying capacity (McCullough 1979), and economic carrying capacity (Caughley 1979). It assumes a lower standing crop of ungulates and a higher standing crop of vegetation (a lower practical or realized carrying capacity) than K carrying capacity. Also inherent is the assumption that with a higher standing crop of forage, the animals are more productive and a higher annual yield or harvest is available (MSY).

"I" carrying capacity is the definition generally recognized by range managers for domestic livestock. When applied to wild ungulate populations and combined with the concept that a high proportion of climax forage species is good, this definition has led to heavy cropping of ungulates in many locations. In commenting on this application, Sinclair (1981), citing Caughley (1976b), stated "Range managers have misguidedly used these plant criteria (decreasers, increasers, and invaders) to determine whether herbivores were overabundant or not by declaring arbitrarily that a high proportion of decreasers was good while a high proportion of invaders was bad." He (Sinclair 1981) added "Unfortunately, this led to management decisions that there were always too many animals (the reason for 30 years of elk culling in Yellowstone [National Park]). These criteria result in the ridiculous conclusion that the only good herbivore population is one vanishingly small."

For practical purposes, intraspecific density-dependent competition for a finite forage resource is the major consideration inherent in most definitions of ungulate carrying capacity. Despite giving at least some "lip service" to other possible environmental variation, the models and graphs of most theorists display a herbivore-forage interaction where the only factor influencing forage production is the degree of use by the herbivores. Models proposed by Caughley (1976b, 1977, and 1979) and McCullough (1979) are typical of widely held views assuming a more or less determinate carrying capacity. Generally, competition for other resources (space, cover, water) has not been considered for ungulates.

The typical density-dependent logistic model (Fig 1.1A) indicates that recruitment rate declines linearly as population density approaches K. Yield, in terms of number of animals that may be harvested while maintaining a stable population, typically peaks around 0.5K (Fig 1.1B). In theory, this occurs because as population numbers approach K, the quantity and quality of food available per capita decreases. Lag effects of a population increase may result in "overuse" of the forage, thereby lowering K.

Fowler (1981) has modified typical logistic models by indicating that most density-dependent change for large mammals occurs at population levels quite close to carrying capacity (Figs. 1.2A and 1.2B). Nevertheless his models in this form retain a fixed carrying capacity (K) influenced only by the herbivore.

In fairness to the modelers, we must point out that, to illustrate a point, they often present a simpler model than they know to be the case. Most realize that environmental

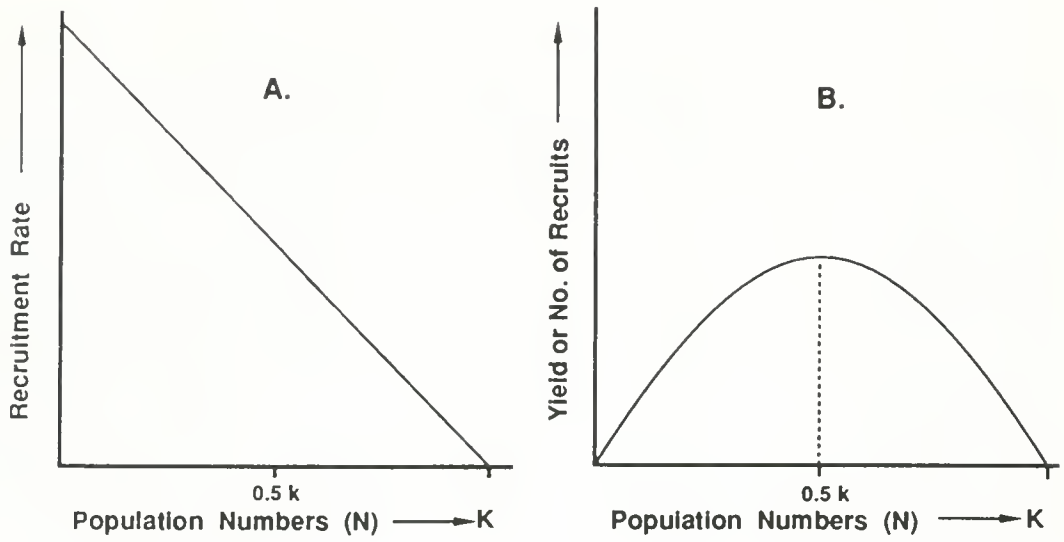


Figure 1.1. Typical density-dependent logistic models for recruitment (A) and yield (B) in relation to animal numbers as an assumed stable carrying capacity (K) is reached.

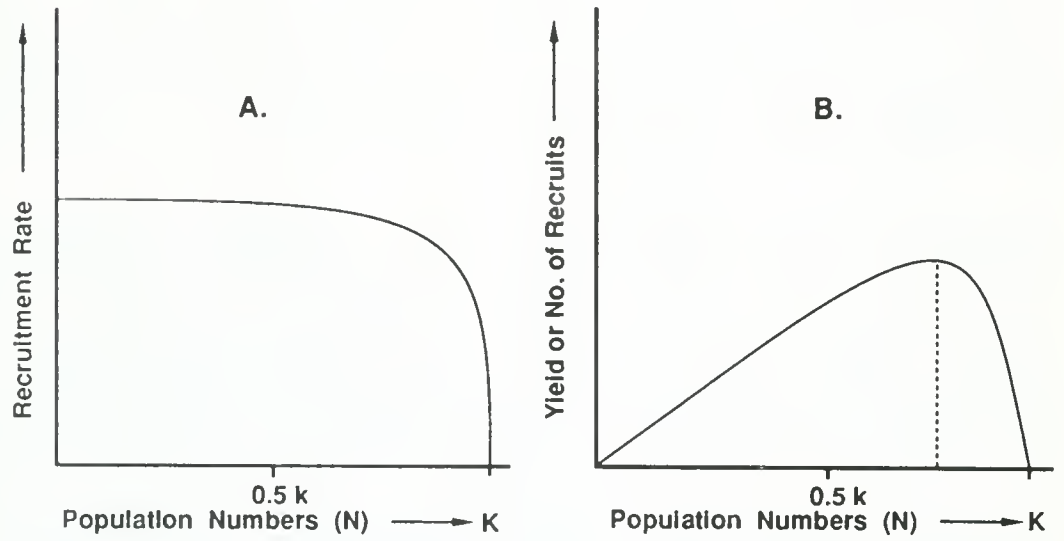


Figure 1.2 Modified density-dependent models for recruitment (A) and yield (B) in relation to animal numbers as an assumed stable carrying capacity (K) is reached. These models assume that most density dependent change takes place near K.

conditions fluctuate independently of animal density and that these fluctuations invalidate simple models. Thus, Caughley (1977, p.197) states:

> "The methods previously outlined for estimating MSY can cope with only a moderate degree of year-to-year fluctuation in a population's condition of life. They will be adequate for most populations. Some populations, however, have a boom and bust economy, increasing when conditions are favorable and crashing to low levels when the environment deteriorates. In this category can be placed most of the species of oceanic fish, and several vertebrates of the northern tundra.
> The simplifying assumption of a steady density, which at best is a dangerous abstraction, almost completely parts company with reality when applied to a boom and bust population. ...In these circumstances density and resources are seldom balanced and one cannot be predicted with confidence from the other."

That caveat was further emphasized by Macnab (1985) in stating "First, in extreme environments (e.g. arid and semi-arid regions) vegetation growth and the recruitment and mortality of large herbivores are highly variable, so that the "equilibrium" is more a mathematical abstraction than an operational reality. ...This changes none of the theory, but makes management more difficult."

Similarly, McCullough (1984:p. 224) indicated that his deterministic model for the George Reserve would not work well where "environmental stochasticity is great relative to the density-dependent response of the environment." McCullough (1984) also stated that "one of the major problems confronting the wildlife biologist or resource manager is the year-to-year variation in habitat quality due to variable amounts of precipitation, severity of winter, presence or absence of an acorn crop, etc." In environmental variable areas, an *ad hoc* strategy is necessary to annually adjust management in response to environmental factors. However, McCullough (1984:p. 225) stated that "Fortunately, most white-tailed deer populations occur in relatively benign environments and respond well to density-dependent management."

Based on findings from our study, we generally agree with the cautionary words of these authors. However, we disagree when they indicate that the assumption of relatively stable environmental conditions applies to most populations. Rather, it seems likely that simplified models <u>may</u> work <u>only</u> for absolutely stable environmental conditions and become increasingly dangerous to apply as variation increases. What

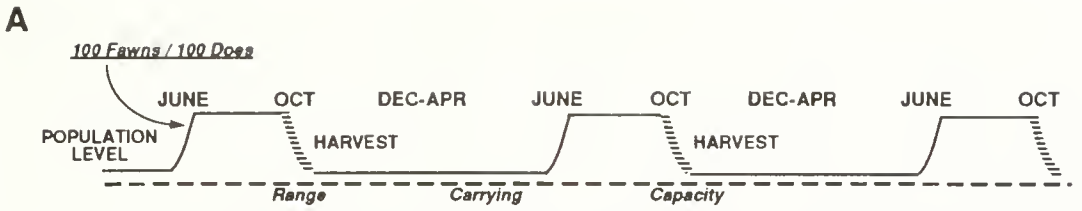
may seem like minor fluctuation becomes magnified upon long-term application of the principles derived from the simple models. Therefore, the simplified models may work for almost no populations. This is particularly true for ungulate populations in arid, semi-arid, or mountainous regions of North America.

Underlying assumptions of fixed forage resources influenced mainly by the herbivores and density-dependent dynamics resulted in the "principles" of compensatory mortality and reproduction. Under this view, reducing the herbivore population below the level of maximal use of forage resources would result in better survival and production by those remaining. The extreme degree to which the "principles" of compensatory mortality and reproduction, density-dependence, and a fixed forage base were carried is indicated by Dasmann (1971) who stated that at the maximum level (ecological carrying capacity or subsistence density), "one deer must die to make room for another".

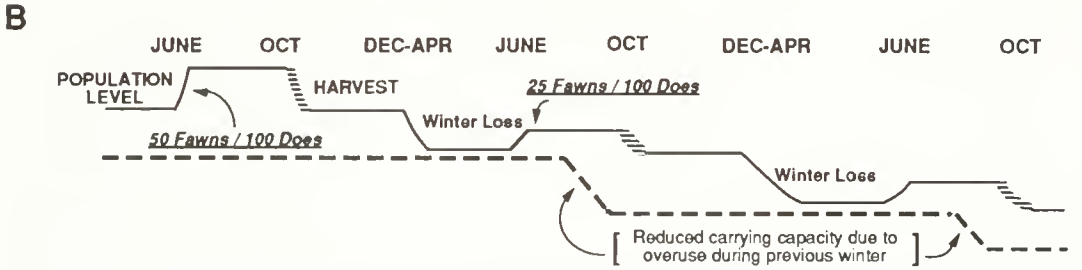
Often, forage resources during winter was considered to be the main limiting factor. For example, Leopold (1966), wrote "The quality and quantity of forage available to a deer population during the most critical season of the year has proven repeatedly to be the basic regulator of population level. Usually this means winter forage, but not always."

The importance of the concepts of forage carrying capacity and especially winter range carrying capacity are illustrated in a typical example (Fig 1.3, Cole 1961) of the way the theory of density-dependent population dynamics and the "principles" of compensatory mortality and reproduction were applied to management of ungulates. Although this management model is simplified, it was essentially the program implemented throughout the United States. Deer needed to be reduced below the "carrying capacity" of their range by hunting. This reduction would result in greater quantity and quality of food for the survivors, thereby increasing their productivity. The reduction of deer numbers below "carrying capacity" would allow the vegetation to "recover", thus actually increasing "carrying capacity".

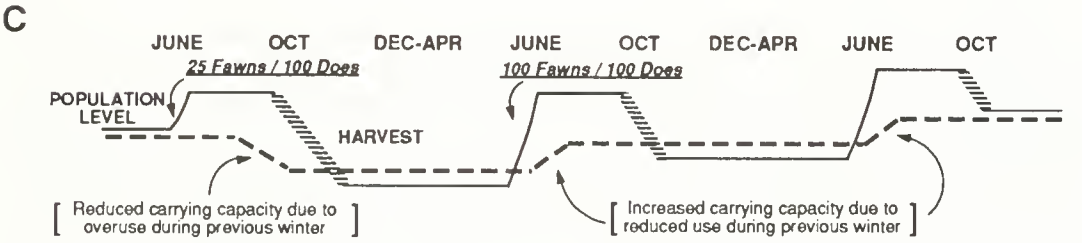
For many years, there was no indication that this model was working. However, this was generally attributed to the belief that adequate harvests had not been achieved or that vegetation took a long time to recover following overpopulation by ungulates (lag effects). Although the model did not appear to be working on many areas, it continued to be widely applied over a broad spectrum of habitats (see McCullough 1979: p. 169), perhaps because no suitable alternative was proposed.



Deer population maintained at winter range carrying capacity by hunter harvests being equal to yearly fawn production



Deer population above winter range carrying capacity and declining due to inadequate hunter harvests



Deer population increasing by harvests permitting increases in range carrying capacity

Figure 1.3. Illustrations of the way concepts of winter range carrying capacity and density-dependent reproduction and mortality were presumed to apply to deer management programs. A. Yearly fawn production matched by harvests maintaining the population in balance with "carrying capacity". B. Inadequate hunter harvest result in "overuse" of range and declining carrying capacity. C. Harvests greater than fawn production allows range to recover, eventually resulting in an increase in carrying capacity (after Cole 1961).

Application of the density-dependent harvest model in deer management during the 1940s to early 1960s did not appear to increase deer productivity, but initially no problems developed as a result of its use. During the late 1960s and early 1970s, however, a widespread decline in mule deer populations across western North America occurred "despite" continued heavy harvest and "recovering" vegetation on many areas. Existing concepts and principles of deer management could not explain the decline (Workman and Low 1976).

Inadequacy of Existing Concepts

Prior to and during the time mule deer populations in western North America apparently collapsed, other scientists were questioning the generally accepted theories of population regulation. Thus, although density-dependent regulation had been assumed to be a reality, Lack (1966) indicated that long-term studies of birds failed to adequately demonstrate empirical evidence for density-dependent regulating mechanisms. He, like many others, was forced to defend density-dependent regulation as a "logical necessity". Similarly, Watson and Moss (1970) wrote: "Clearly, density-dependence and equilibrium levels are statistical concepts, not necessarily biological reality." Ehrlich and Birch (1967) questioned the concept of a "balance of nature" and the overriding importance of density-dependent population regulation. Birch (1971) continued to emphasize the importance of environmental and genetical heterogeneity in population regulation.

From a mathematical and statistical perspective, Maelzer (1970) and St. Amant (1970) showed that regression analysis previously used to "prove" or detect density-dependent regulation did not necessarily do so. Random variation could give the same results as density-dependent regulation when the often used technique of regressing log population density against log previous population density was employed. Thus, the relationships between population density and growth rate as proposed by Tanner (1966) were also subject to question.

If the concept of density-dependent population regulation was questionable, at least in some areas or for some populations, then harvesting theory based on that concept would also be questionable. The "unexplained" decline of mule deer on our study area and elsewhere during the early to mid 1970s led us and others to question these concepts as they related to mule deer in much of Montana.

In concluding this review of past studies, theories, and problems, we note that most data collected or analyzed to form, "prove", or verify prior theories of population regulation came from short-term studies, introduced or founding populations, and laboratory, penned, or island

populations. Most studies were done purposefully where environmental variation was minimal, or in the case of laboratory populations, the environment was held stable.

Ecologists, especially these emphasizing the concept of equilibrium (Caughley 1981a), generally follow the tenet that experimental perturbation of the population is necessary to determine the effects of various factors on population dynamics and their importance in regulation. Laboratory or penned populations are often used because it is easier to hold most factors stable while experimentally varying a single factor. The problem with this approach is that it sacrifices general applicability and reality to obtain strength in precision. This problem has been recognized (Levins 1966, Smith and Fowler 1981) but the complexities of dealing with the multi-factorial "real world" have been daunting and the current fad is precision.

Van Ballenberghe (1980) characterized much of the work on population regulation as ... "people trying to force ecological events into the conceptual framework of classical physics and systems theory." He also indicated that most work stresses stability and employs models. Further, the model is usually constructed first and the theorist scrambles to look for field data that will confirm the model's predictions.

Because our studies were supported by a management oriented agency, our research contained an inherent bias toward applicability in the "real world". Attempting to track the many varying factors inherent in "real" populations was no less a challenging task for us than for anyone else. We found, however, that while uncontrolled variation ("chaos") is intimidating and incomprehensible when followed for short periods, patterns of population behavior begin to emerge after longer periods of time. Conclusions may suffer some degree of reduction in precision, but they are applicable to the real situations in which management must occur.

The most recent phase of our study (1975-1987) began with an established "natural" population and the beginnings of long-term data. As opposed to many previous study situations, the environment on our study area was extremely variable. Perhaps that, in itself, resulted in our somewhat different conclusions about and interpretations of population "regulation" in deer. For mule deer, at least, a variable environment is not necessarily atypical. Thus, our results and conclusions should have some general applicability.

Because existing theories of population regulation and management philosophy did not appear to explain mule deer population trends, we collected and analyzed data with the suggestion of Chitty (1967b) in mind: "Perhaps ecologists of

the next generation will be more successful [in explaining population regulation] ... They might start by doubting the truth of everything that has so far been written on the subject, including the ideas of the present reviewer."

When examined from a broad perspective, the many theories are not all that far apart (Murray 1979) and are not necessarily mutually exclusive. Perhaps one failing of regulation theory thus far has been the tendency to draw into opposing camps and look for and promote a unifying theory or model which may not exist.

An Alternative Theoretical Framework

We begin explaining our proposed theoretical framework with a discussion of the perspective from which we reached our conclusions. This is necessary because many past theoretical disagreements (even about the meaning of the same data sets) have been rooted in the different perspectives of the contending writers. The reader must be aware that the interpretation of our data is based on the following conditions:

1. The environment and especially the weather is extremely variable. This was also reflected in vegetation-forage production.

2. The area was not fenced and was surrounded by adequate "dispersal sinks".

3. An effective, facultative natural predator coexists with the deer on this area.

4. Human predation (hunting) in varying degrees of effectiveness is practiced on the area.

5. We examined attributes of the environment concurrently with deer population dynamics, behavior, and habitat selection and use.

6. We related our information to other studies in Montana and elsewhere as we proceeded. We did not focus our thinking entirely on one study population.

Most general theories of population regulation have emphasized stability and the Nicholsonian "balance of nature". Ehrlich and Birch (1967) have criticized this perspective, and for the most part, we agree with their criticisms. We, by virtue of exposure to our study population, emphasize variability in our conclusions. On the other hand, we also have a broader perspective. Species populations over this planet are faced with a wide variety of possible environments

or habitats. These populations can exist in a variety of forms in some environments and not at all in many other environments. This is true even within smaller areas such as the State of Montana. Within the environments they occupy, population characteristics and dynamics vary according to the environment; some are relatively stable, some are relatively variable, and most may function somewhere between the two extremes. As Murdoch (1966) stated: "In attempting to formulate general theories of population control, ecologists are faced with the problem that every population is, in some sense, unique".

Our analysis, interpretation, and writing often focuses on the importance of the individual animal. At times, this makes both writing and reading unconventional and difficult. A focus on the individual is sometimes necessary, however, to understand and explain dynamics. A population is generally an artificial entity; it has no life of its own. The dynamics of a population are made up of the sums and interactions of the histories and fates of individual animals. For variable populations in variable environments, insight is often lost or obscured by compressing data into means, even when measures of deviation are included. In some cases, few if any animals exhibit mathematically average behavior, performance, or fates. The sum of this variability may lead to somewhat predictable phenomena, but to understand it or to make management adjustments, one must understand individual histories.

This variability also affected our data analysis and presentation in other ways. Much of the data did not meet the stability assumptions inherent in "classical" analytical techniques of demographic investigation. Analysis and presentation of data in those forms is necessarily missing here. We also, by necessity, present few precise and deterministic models.

Because "there is nothing new under the sun", many or most of our interpretations and conclusions have been hinted at or boldly stated by others. The reader may find similarities in our views and those of Thompson (1929), Andrewartha and Birch (1954), Milne (1958), Ehrlich and Birch (1967), Birch (1971), Sinclair (1974), White (1978), Murray (1979), Botkin et al. (1981), Cockburn and Lidicker (1983), Ostfeld et al. (1985), and Lidicker (1988) among others.

The Population-Habitat Model

We propose that the total, unique environment each population occupies establishes its characteristics and dynamics. Further, no 2 populations on the same area, but at different times, will exhibit exactly the same behavior, even

if their initial numbers are the same (see Petrusewicz 1963). This is due to both the unique nature of individuals and the environment over time. Heterogeneity of the environment in both space and time is an important concept in our interpretations.

We also support a multi-factorial model of population dynamics. The importance of each factor, the intensity and frequency at which it operates, and the interaction of factors all vary with the species, population, and environment. There are elements of all previous theories within our alternative. A principal difference is that we do not emphasize one aspect to the extent of excluding others.

The habitat portion of the model (Fig. 1.4) contains both a relatively fixed-stable component and a dynamic-variable component. The fixed-stable component of the habitat model includes the following factors: location (latitude, longitude, altitude), general climate zone, topography, soil fertility, vegetation, and habitat structure and heterogeneity. To the extent that these factors can change, they generally do so over a long period of time.

The dynamic-variable component of the habitat model includes the following factors: weather and forage variability, predation, hunting, inter- and intraspecific competition, and the effects of man's activities on the habitat. In some cases, man's activities can also impact the fixed-stable habitat base. Variability of weather affects the length and amplitude of periods of positive and negative energy balance, forage production and quality, and the operation of other variable components of the model such as predation, hunting, and interspecific competition.

The animal component of the model (Fig. 1.4) contains the genetic, morphological, physiological, and behavioral characteristics of animals that determines their resource requirements. The interaction of resource requirements with resource outputs and availability determines *individual* animal strategy.

The submodel of individual animal strategy (Fig. 1.4) has both behavioral and physiological components. Behavioral responses to the interaction of resource requirements and resource outputs include: parturition territoriality, dispersion or home range location, habitat use patterns, emigration-immigration, activity patterns, food habits, and movement patterns. These all have physiological consequences including: animal size, condition, and reproductive strategy. Behavioral and physiological responses to the interaction of habitat and animal components determines recruitment and

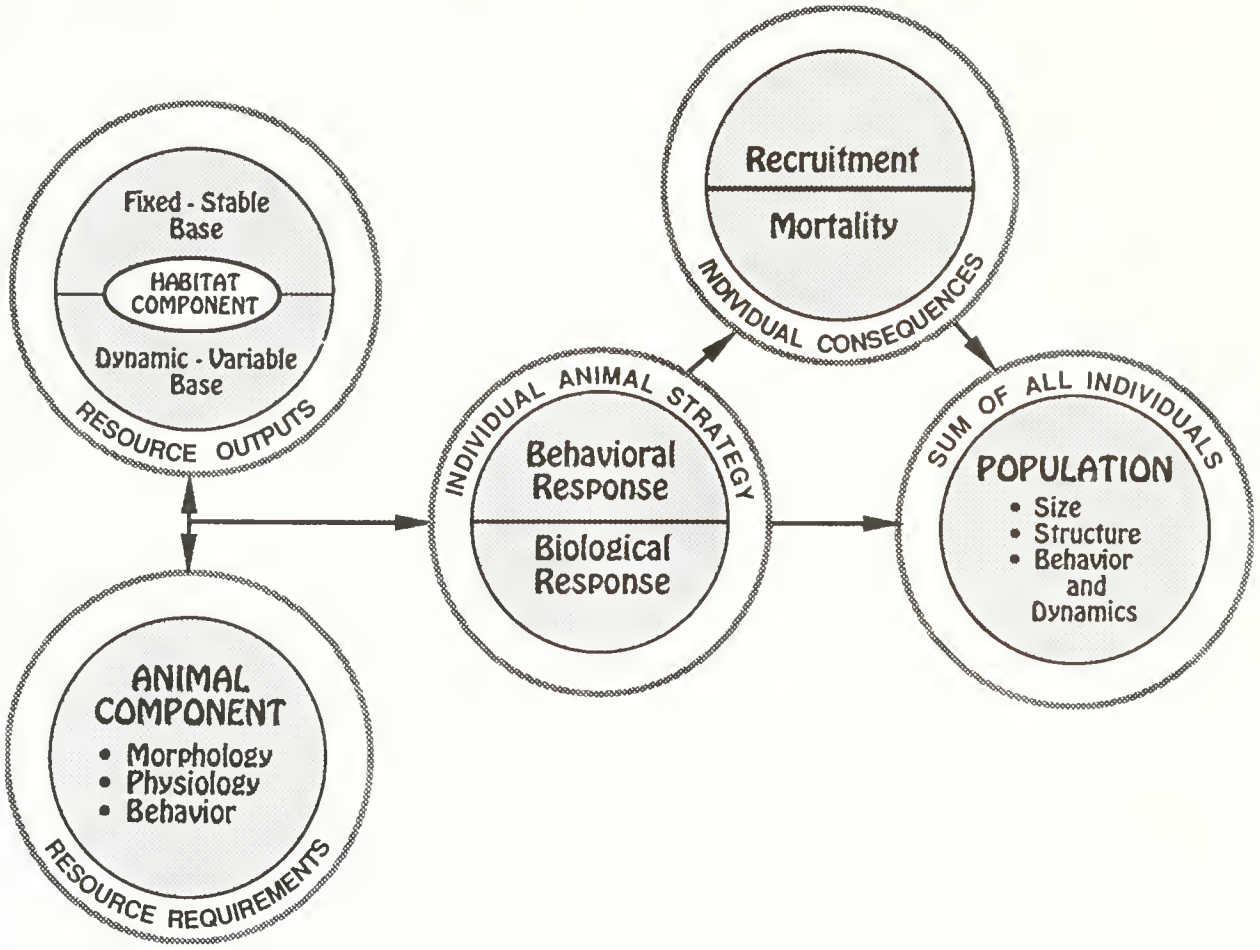


Figure 1.4. Our model of animal-habitat-population interactions illustrating important components and pathways of interactions and consequences.

mortality consequences to the *individual* animal. The sum of those individual strategies and consequences determine *population* size, structure, behavior, and dynamics (Fig. 1.4). The behavioral, physiological, recruitment, and mortality submodels all contain both relatively stable and variable components that interact with each other and with the habitat model.

Each component of the overall model (Fig. 1.4) can be further subdivided with more detail. For instance, predation, as part of the variable environment, includes such factors as population level of coyotes, deer, and alternate prey; all the natural factors affecting those populations (including weather, livestock grazing, etc.); and the effect of humans (predator control).

No *one* factor can be said to be *the* ultimate factor regulating the population. Interaction of factors is very important. Overall, however, we believe that variable weather interacting with the fixed habitat base is the ultimate factor behind most changes in recruitment and mortality. Other factors, such as predation, act as variable proximate factors within the overall model. The removal of one or more proximate factors such as predation, hunting, or emigration, however, could result in observation of more "classical" density-dependent population responses.

The relative contribution of fixed-stable and dynamic-variable components of the model to population characteristics is illustrated by the 3 Montana mule deer populations presented in Fig. 1.5. We propose that the fixed-stable habitat base establishes potential population density (the high) and explains why abundance varies from place to place. The interaction of dynamic-variable habitat and population components establishes the normal range of population density below that potential and the actual position of the population within that range at any given time. Thus, the dynamic-variable components explain fluctuations in numbers within a population.

The data for our study population indicated that interaction of a changing relative energy balance and availability of permanent suitable habitat (space) limited its growth. Food was only one part of the energy balance equation. Density-independent fluctuation in weather was the major factor influencing forage abundance and quality, energy requirements, and deer population dynamics. There was little or no feedback between deer density and forage abundance or quality. Thus, although density-independent variation in forage quantity and quality affected population growth, seldom, if ever, did the population reach levels where

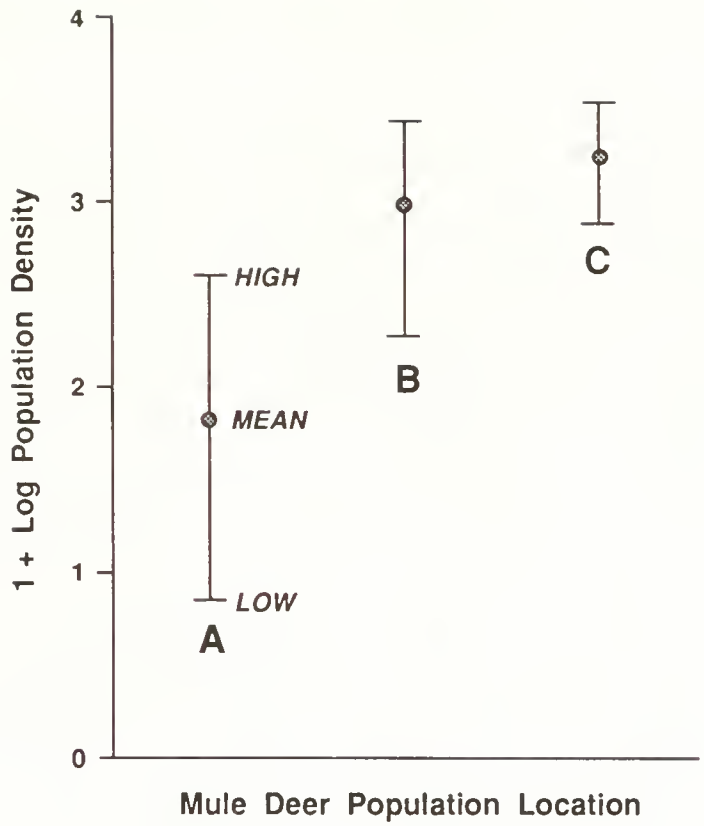


Figure 1.5. Mean and range of densities for 3 Montana mule deer populations. A=Cherry Creek (Wood et al. 1989); B=Missouri River Breaks (this study); C=Northwest slope of Bridger Mountains (Pac et al. in prep.)

density-dependent intraspecific competition for forage could have been important.

Our data also indicated that "territoriality" of females during parturition (also see Ozoga et al. 1982 for white-tailed deer) functioned to determine home range establishment for the entire population. This "territoriality", at times, also resulted in emigration, which helped limit population growth rate.

Because the environment was heterogeneous and habitat quality varied across the area, home range location (space) and use influenced recruitment and mortality rate of individual animals. During "good" conditions, deer survived and recruited fawns in "marginal" areas. During "poor" conditions, deer with home ranges in marginal areas not only failed to recruit fawns, but were subject to higher mortality

rates than deer in "core" areas. Recruitment and mortality were properties of individual animals in individual home ranges.

Occasionally, mortality was high when density was high. This was not really the result of density *per se*, but the result of density-independent changes in energy gain and loss related to variable weather patterns. Seasonally and annually, variable weather modified habitat quality, structure, and its ability to support deer. When weather conditions were conducive to deer living in "marginal habitats", survival remained high despite high deer density. Also, few deer lived in marginal areas unless density was high. Thus, when density was high, more deer were vulnerable to density-independent changes in weather. "Carrying capacity" fluctuated widely and annually, usually as a result of density-independent factors (especially weather).

Our model of population dynamics may be unsatisfactory to some, especially those who would prefer to "force" ecological events into mathematical formulae. Although we did not observe "classic" density-dependent population responses, they may be relatively more operational in stable environments and those lacking predators or dispersal sinks. However, there are many other types of populations and situations that must be dealt with by managers. Often, knowledge of what proximate factors are affecting populations is more important than what the ultimate regulating factor is under precisely specified and fixed conditions. We most hope to convince the reader that dogmatic, deterministic, or fixed views are often not helpful or widely applicable. A framework of general principles may apply overall, but interpretation and application of those principles must be made within the context that each population is a unique product of its total environment.

CHAPTER 2

APPROACH AND METHODS

Early Studies

The data on which this report is based were derived through a series of studies of broadly different objectives and intensity, encompassing a variety of methods. In this chapter, we present a general overview of our approach and the methods employed in obtaining and analyzing the major data sets. More detailed information is provided by references cited or in presentation and analyses of specific data.

Generally, the studies comprised 3 phases: (1) intensive studies emphasizing range use and relationships of mule deer, elk, and cattle during 1960-1964 (Mackie 1965, 1970); (2) extensive studies focusing primarily on mule deer population characteristics and trends in relation to range condition from 1964 through 1974 (Mackie 1973, 1976); and (3) intensive studies of mule deer population ecology and habitat relationships during 1975-1987.

The early studies provided baseline data on habitat characteristics of the study area, distribution, movements, use of specific habitat/vegetation types and topographic/physiographic sites, activity patterns, food habits, and population characteristics and trends for mule deer from 1960 through 1963. These studies were primarily descriptive. Data on vegetation were obtained through classification and measurement of vegetational characteristics of habitat/vegetation types, and annual measurement of utilization and condition trends for major shrub species browsed by deer on permanent transects. Data on deer were obtained by systematic observations along vehicle routes throughout the area, recording plant species eaten at feeding sites, analyses of ruminal contents of deer collected and shot by hunters, and conducting checking stations and field check of hunters to determine distribution, numbers, sex and age composition, and condition of deer harvested (Mackie 1970).

Data on population size and characteristics were obtained primarily through counts and classifications of deer observed along the vehicle routes and from harvest information. Aerial surveys and observations were limited and provided only supplementary data on range use and population characteristics until winter 1963-64 when the entire study area was surveyed using a helicopter to count and classify deer and elk. Only 16 mule deer and 3 elk were marked, none with radio collars.

Comparisons of ground and aerial counts during 1960-64 indicated that helicopter surveys, flown for complete coverage following snowfall in early winter when most deer used open ridgetop habitat, provided an effective method for determining numbers and sex and age composition of mule deer on the study area. Because of a need for continuing information on population characteristics and trends in management of mule deer in breaks habitat, and termination of intensive studies, the helicopter surveys became the primary method of study during the second, extensive phase.

Early winter surveys were conducted in most years from 1964 through 1975. Exceptions included 1968, 1969, when classification counts were made by the area management biologist with a fixed-wing aircraft, and 1972, when mild, dry weather precluded flying until late winter. Overall, these data provided estimates of population size and composition and trends in relation to range/environmental conditions throughout the period (Mackie 1973, 1976).

Measurement of utilization and condition trends of major browse species was also continued in spring of each year on established transects. In addition, 5 permanent point-center-quarter transects measuring shrub composition, density, and plant size were established on the area during 1971 as part of a study of ecological characteristics of fragrant sumac in Montana (Martin 1972).

Mule deer harvests were monitored in a limited manner through field reconnaissance during hunting seasons and the statewide harvest survey for the hunting district which includes the area.

During 1972-1975, 2 graduate thesis research studies were completed on our supplementary Nichols Coulee Resource Conservation Area (NCRCA) study area (Knowles 1975, Komberec 1976). Designed to evaluate range relationships of mule deer and elk within a rest-rotation grazing system, these studies included aerial population surveys similar to those conducted on our primary study area and use of marked and radio-collared deer in studies of habitat use.

Recent Studies

The third phase, beginning in 1975, was precipitated by the failure of existing knowledge and theory about mule deer habitat relationships and population dynamics to explain population phenomena observed on the study area and elsewhere. Our study area and the 15 years of baseline data available provided exceptional opportunity to conduct the intensive, long-term population studies we believed necessary to develop an improved understanding of the process and mechanics of

population regulation in mule deer. In undertaking those studies, we also believed it necessary to closely examine and perhaps rethink current knowledge of basic mule deer population biology and ecology. Thus, we did not attempt to test specific hypotheses; nor did we employ the rigid techniques used in much scientific hypothesis testing. Instead, we approached our intensive studies more in the manner of natural historians (Bartholomew 1986, Greene 1986), with some direction but also relying on "serendipitous and unexpected" results (Greene 1986). In taking this approach, we focused heavily on obtaining as complete and detailed data as possible on population ecology. Thus, much depended on our ability to obtain detailed and reasonably accurate data on mule deer population characteristics and trends.

Beginning in 1975, complete-coverage surveys employing both helicopter and fixed-wing (Piper SuperCub) aircraft were flown during autumn and spring as well as in early winter. From 1976 through 1983, fixed-wing surveys were also conducted in July. During all surveys, numbers, sex, age, group size and composition, location, and other data were recorded for mule deer and most other major species observed. As marked deer became available, observations of those deer also were recorded.

During summer, autumn, and early winter surveys, deer were classified as fawns (<12 months of age), adult females, yearling males (12-24 months of age), and mature males (>24 months of age). Yearling and mature males were distinguished by gross differences in antler size based on experience in aging and measuring antlers of hunter-killed deer. We did not attempt to distinguish yearling from mature females. Deer were classified only as adult or fawn during spring.

During 1975-1986, 416 different deer were captured and marked with individually-recognizable neckbands or radio collars. Sixteen of those were recaptured and recollared once, 2 were recaptured and recollared twice. Overall, 202 were first captured as newborn fawns, 71 were 6-8 months of age, 119 were adult females, and 24 were adult (>18 month) males. Twenty seven of the newborn fawns (14 males and 13 females) and 19 (9 males and 10 females) marked at 6-8 months were offspring of marked does. Ages were assigned to all deer older than newborns on the basis of tooth replacement and wear criteria (Robinette et al. 1957). Other procedures followed in handling deer and recording data have been described by Hamlin et al. (1982) and Riley and Dood (1984).

Newborn fawns were located from the air and captured by ground crews directed to the site by radio (Riley and Dood 1984). One hundred seventy-eight were fitted with

radio-transmitter collars and numbered metal eartags; 24 were marked only with eartags or eartags and a vinyl earflag.

Most deer over 6 months of age were captured using a drive net (Beasom et al. 1980); a few were captured with cannon nets (Hawkins et al. 1968) and a hand-held net gun (Barrett et al. 1982). We marked 89 with radio-collars, 124 with 10 cm-wide, individually recognizable neckbands, and 1 with eartags only. Seven fawns, radio collared as newborns, were later recaptured; 2 were refitted with radio collars and 5 with individually recognizable neckbands. Two adults, originally marked with neckbands, were equipped with radio collars upon recapture. Four adult females had their radio collars replaced once, 2 others had theirs replaced twice. The effective life of radio collars varied, but most fawn transmitters functioned for 1-2 years while those on adults lasted 2-5 years.

During most of the study, we attempted to relocate all radio-collared deer at least twice monthly using a PA-18 Piper Super Cub with antenna mounted on the wing strut. Many were relocated more frequently. Some relocations, especially of newborn fawns which we attempted to locate at 2-3-day intervals, were made from the ground. Most relocations were made during the period one-half hour before sunrise to 2 hours after sunrise. A minor number of relocations were made during mid-day and evening hours, but no relocations were made during periods of darkness. Visual observations of the deer were made on approximately 83% of aerial radio-telemetry relocations. Relocations of radio-collared as well as neck-banded deer were also recorded from observations during the course of other fieldwork, including aerial population surveys and flights associated with efforts to locate and capture fawns in June or other deer during winter. Occasionally, special aerial searches were conducted to attempt to locate neckbanded deer that had not been observed for some time.

All relocations were recorded to the nearest 3.2 ha from gridded aerial photographs. Social groupings and associations, numbers of fawns-at-heel with marked females, and other pertinent data, including habitat use during some years, were recorded when possible. Locations and other data were also recorded for all unmarked deer as well as for other major species observed during relocation flights. Radio-collared coyotes (Pyrah 1984, Hamlin et al. 1984) and radio-collared and neck-banded elk on the area were monitored; data were recorded in the same manner as for deer.

We obtained 9,841 observations of 354 marked deer during 1 June 1976 - 31 May 1986. In addition to population estimates, relocations of marked deer provided data for estimating seasonal and annual reproduction, recruitment, and

mortality rates, both generally, and specific to sex and age classes of deer. They also provided information on movements and home range, social structure, and behavior.

Biological materials and physical measurements were obtained from deer killed by hunters and coyotes, trapping mortalities, special collections, and deer found dead on the area. When possible, sex, age, location, and cause of death were recorded. Age was assigned on the basis of tooth replacement and wear, and later confirmed or adjusted by cementum analysis (Gilbert 1966) of an incisor extracted from deer 2 years of age and older. When available from carcasses, kidneys and attached perirenal fat were collected and a kidney fat index (KFI) was calculated following Riney (1955). Femur fat samples were taken from collected and coyote-killed deer; color and consistency was recorded and percent fat content was measured using the reagent-dry assay technique (Verme and Holland 1973). Data on animal condition and trends were also obtained by recording field-dressed weights and antler measurements (French et al. 1956, Robinette et al. 1973) for samples of deer killed by hunters.

Reproductive tracts were collected from females taken in special collections. Incidence of ovulation, corpora lutea of pregnancy, and fertilization rates were determined (Cheatum 1949). Fetal ages were assigned from crown-rump measurements based on growth rates of known-age fetuses (Hudson and Browman 1959). Further data on reproductive potential were obtained during fawn capture operations and from fawn-at-heel ratios recorded for all productive females during June (Hamlin et al. 1984). Pregnancy rate also was estimated by recording the appearance and behavior of all females observed during mid June (Ozoga et al. 1982, Hamlin et al. 1984). Age-specific fawn production and survival was evaluated using fawn-at-heel ratios and percent pregnancy among individually marked females of known or assigned age (Hamlin and Mackie 1987).

Seasonal and annual mortality rates were calculated from several data sets. When available, mortality rates of marked deer were used. Fawn mortality rates were estimated from deaths in a radio-collared sample and changes in fawn:female ratios recorded in seasonal population surveys. Differences between seasonal and annual population estimates also provided estimates of mortality rates. Information on relative rates and composition of hunter harvests for the hunting district including the study area were available from statewide questionnaires and telephone surveys (Cada 1985). Additionally, hunter check stations and field checks were conducted during 1960-1965 and 1976-1987 to determine relative numbers, sex, age, and condition of deer harvested on our study area each year.

The locations of deer and other species observed during full-coverage aerial surveys, radio-relocation flights, and other operations were recorded as the mid point of a 3.2 ha grid block. Those locations were transformed to Universal Transverse Mercator (UTM) coordinates for analysis of distribution, habitat use, and home range and movements. Seasonal and annual home ranges and movement patterns as expressed by the minimum convex polygon (Mohr 1947) and average activity radii (Hayne 1949), were calculated using TELDAY software (T.N. Lonner and D.E. Burkhalter, Users manual for the computer program TELDAY, Mont. Dept. Fish, Wildlife and Parks, unpubl.). Habitat use was evaluated using a block (cell)-analysis technique (Porter and Church 1987, Wood 1987) in which use was compared with availability (Byers et al. 1984) using Chi-Square tests (Everitt 1977). Analyses of distribution, movement, home range, and habitat use as well as social organization included only data obtained through 1984 when field studies were reduced to focus on data analysis and reporting.

Comparative data on population characteristics and trends for adjoining breaks habitat were obtained by special aerial surveys and continuing the full-coverage, helicopter and fixed- wing surveys on the nearby Nichols Coulee Resource Conservation Area (NCRCA) study area.

The NCRCA, located north of the Missouri River, 3.2 km northeast of our primary study area, served as a comparative study area for mule deer. This area, described by Knowles (1975), is also "River Breaks" habitat, but is somewhat more arid, almost totally lacks the Douglas fir (*Pseudotsuga menziesii*) vegetation type, and is physiographically characterized by major drainages that are steeply cut in a north-south orientation such that steep slopes adjacent to the river are primarily south-facing.

River bottoms on and adjacent to the primary study area, described by Allen (1968), were used to obtain comparative population data for white-tailed deer.

To assess possible effects of predation and interspecific competition on population ecology and dynamics of mule deer, we collected data on other species inhabiting the study area, including elk, white-tailed deer, pronghorn antelope, coyotes, lagomorphs, and various small rodents. Data on elk and coyote numbers, distribution, and habitat use were recorded during all complete-coverage surveys for mule deer. Special aerial surveys were flown to count and classify whitetails on the Missouri River bottoms. Aerial surveys of antelope on the area and adjoining plains were flown in late summer by the area management biologist. Siren and den area surveys of coyotes by Pyrah (1984) and project personnel provided coyote

population estimates. Vehicle headlight surveys to obtain estimates of lagomorph abundance were made 2-4 times each year on established routes through the area and adjoining plains (Trout 1978, Hamlin et al. 1984). Small mammal abundance was determined from 2 permanent Sherman live-trap grids (Trout 1978, Hamlin et al. 1984).

Annual forage production was estimated during 1976-1986 by clipping vegetation within 2 X 5 dm and 4 X 10 dm plots in two stands in sagebrush-grassland and measuring current annual growth of shrubs on two transects in the Douglas fir-juniper type. General principles involved in establishing production estimates for herbaceous forage followed Pieper (1978). Estimates of production by shrubs generally followed Basile and Hutchings (1966) and Lyon (1968). Modifications made and more detail on techniques are discussed by Jorgensen and Mackie (1976).

Browse utilization trends were measured annually in spring on transects (Cole 1958, 1959) established throughout the study area during 1959-1961. Relative changes in abundance of shrub species through the years were determined by monitoring tagged plants on browse transects, measurement of tree-shrub coverage on line-intercept transects established in 1963 (Mackie 1970), and measurement of shrub density and plant size on point-center-quarter transects established in 1971 (Martin 1972).

Food habits of mule deer were determined by examination of feeding sites and rumen analysis during 1960-1964 (Mackie 1970) and rumen analysis during 1976-1987.

Data from the Roy 8NE weather station were not detailed enough to calculate several established winter severity indexes prior to 1967. To have an index of winter severity for all years of study, we constructed our own index. This constructed index gave values relative to the mildest recorded winters on the area and was calculated as follows:

$$WSI = (Tw - Tc) + \left(\frac{Sc - Sl}{5}\right)$$

where:
- WSI is winter severity index
- Tw is warmest recorded mean winter (Nov-Mar) temperature in degrees F
- Tc is current mean winter temperature
- Sc is total snowfall for the current winter in inches
- Sl is lowest recorded total winter snowfall in inches

Our winter severity index (WSI) gave values highly correlated ($r=0.92$, $n=19$, $P<0.01$) with values from a modified Leckenby Index (Leckenby and Adams 1986), required less detailed data, and could be calculated for a longer series of years.

Statistical procedures generally followed Snedecor and Cochran (1967) and Zar (1984). Analyses were conducted using the Montana State University computing service and personal computers. Statistical packages used included the Statistical Analysis System (SAS) (Ray 1982) and MSUSTAT (Lund 1983).

Estimating Population Numbers

Like most mule deer habitats in the northern Great Plains, our study area was "open". Grassland - low shrub vegetation covered about half of the area and stands of coniferous vegetation were typically small or patchy, distributed along slopes, and held only scattered to low densities of trees that rarely exceeded 15 m in height. The area also comprised a relatively discrete population-habitat unit because mule deer were usually distributed on yearlong individual home ranges scattered throughout the area. During late autumn, winter, and especially early spring, the deer tended to group locally and utilize uplands and open ridgetops such that observability and counting efficiency was high. Because of this, aerial census provided a highly efficient and effective means of measuring population characteristics and trend.

Our use of complete-coverage surveys eliminated possible bias resulting from sampling design. Quadrat and transect sampling require precise sampling systems that ensure random and representative effort over complex mosaics of topography and vegetation. They are also subject to the same visibility bias of any census that results in fewer animals seen than actually occur (Caughley and Goddard 1972). Our counts always represented an absolute minimum estimate of the number of deer on the area. To develop a reasonable total population estimate, we had only to account and adjust for visibility bias. This we accomplished by developing observability indices (estimates of proportions of total deer observed) relative to season, survey conditions, aircraft, and observers. We also collected data on a variety of population characteristics for comparison and reconciliation with population estimates through arithmetic modeling (Mackie et al. 1981). A major thrust of our intensive studies during 1975-1987 was to further develop and test this approach to population estimation.

Normally, to obtain the most accurate population estimates, multiple aerial surveys are recommended for each sampling period. The number of replicates required depends upon the count as a proportion of the total population and the number of marked deer as a proportion of the total population (Rice and Harder 1977). As with most studies, our funding was limited. Because of this, our earlier experience, and our objective of concurrently estimating deer numbers and collecting other types of data, we directed our efforts toward 3-4 population surveys at different times of the year rather than 3-4 replicates during one period.

Although this approach initially reduced our confidence in any one estimate, over time it had the advantage of providing estimates at shorter time intervals that could be reconciled with sex and age composition and mortality data from other sources. Also, because the survey data were collected over many years, data sets were developed that could be analyzed similar to replicate counts made near the same time in one year. For example, the surveys flown with the same pilot and observers during late December or early January each year from 1980 through 1986 could be used as replicates to determine the average percentage of deer observed at that time of the year. Although the percentage of the population marked (generally 4-9% during winter and spring) was lower than desirable (Robson and Regier 1964), the total count as a percentage of the total population (60-83%) was much higher than usual.

The 3-4 population estimates made each year during 1976-87 generally supported one another and, when correlated with total counts, provided support or basis for improving estimates for earlier years when population size was estimated from a single complete coverage survey in winter or spring. Any estimate, before being finalized, had to include reasonable reconciliation of numbers in the various sex and age categories. These accounted for proportion observed in concurrent classifications as well as known or estimated mortality and natality based on hunting statistics, survival of marked deer, dispersal of marked deer, and population numbers and composition from prior and subsequent estimates. Our estimates based on the Lincoln index for years when adequate numbers and distribution of marked deer were present were seldom far from numbers estimated from known or estimated natality and mortality, especially during early winter and spring.

The proportion of marked deer observed during aerial surveys (observability) was generally consistent within a season from year to year when the same pilot and observer were used. Observability was most consistent and precise and population estimates were most accurate during early winter

and spring. Population estimates for July, a time when yearlings were dispersing and males were more observable than females, were considered reliable only as a general index to population size. Considering their potential shortcomings, the July estimates were relatively accurate (Table 2.1). Observability of deer during July appeared to increase with population size up to a density of about 3.9 deer/km^2.

Observability of deer during autumn surveys also appeared to increase with density to a population of at least 3.9 deer/km^2. Once population level was accounted for, observability was lower during surveys flown with pilot D than with pilot B (Table 2.2). Observability was generally consistent, however, for each pilot.

The greatest deviations between Lincoln and modeled population estimates for autumn (Table 2.3) occurred in 1983 and 1985. Sex and age composition in modeled estimates (Appendix A) had to be consistent with estimates for the previous spring and the subsequent early winter, given natality and mortality during the period. We considered the Lincoln estimate for autumn 1983 inaccurate because 1) bad weather caused a 5-day break in flying mid way through the survey, allowing deer movement between areas, and 2) apparent drought-related movement of some deer from adjacent prairies onto the study area occurred in late summer. The Lincoln estimate for autumn 1985 was considered inaccurate because an unusually early snowstorm resulted in some deer moving from summer to winter ranges during the survey. Overall, the average deviation between the Lincoln and modeled estimates for autumn was 13.1%. When 1983 and 1985 were excluded, the average deviation was 10.0%. Generally, precision for the proportion of marked deer observed during autumn was less than that for winter and spring, even when the same pilot was used. This probably reflected more variable conditions during autumn and the influence of deer density on observability.

Observability of deer during early winter helicopter surveys was very consistent from year to year (Table 2.4). An average of 66% of all marked deer were observed in surveys flown with pilot A during 1977-1979 and this estimate was precise (CV = 1.8%). During 1980-1986, pilot B was employed, the surveys were flown at an altitude 20-30 m higher than in previous years, and an average 78.8% of the marked deer were observed. Again, the coefficient of variation was low (6.6%). Flying at slightly higher altitude apparently enabled us to observe and record deer which previously had moved before the helicopter over ridges and into areas we had covered earlier. Observability was as high or higher during surveys in years of no snow cover (1981) as in years of complete snow cover

Table 2.1. Mark-recapture population estimates (Lincoln Indexes) for mule deer from aerial surveys on the Missouri River Breaks study area, July 1979-1984.

Date	Aircraft	Pilot	Conditions	Total Deer Observed	Marked Deer Observed	Marked Deer Present	Proportion Marked Deer Observed	Population Estimate	Modeled Estimate
07-79	PA-18 Super Cub	B	not recorded	157[a]	12	50	0.240	654[a]	640[a]
07-80	PA-18 Super Cub	B	not recorded	354	19	60	0.317	1118	810
07-81	PA-18 Super Cub	B	not recorded	354	32	79	0.405	874	975
07-82	PA-18 Super Cub	B	not recorded	413	30	75	0.400	1033	985
07-83	PA-18 Super Cub	B	not recorded	587	29	71	0.409	1437	1115
07-84[b]	PA-18 Super Cub	B	not recorded	184	9	56	0.161	1145	1040

[a] All numbers in these columns are adults only.

[b] Flights covered all portions of area, but much less intensively than previous flights.

Table 2.2. Mark-recapture population estimates (Lincoln Indexes) for mule deer from aerial surveys on the Missouri River Breaks study area, autumn 1977-1986.

Date	Aircraft	Pilot	Conditions	Total Deer Observed	Marked Deer Observed	Marked Deer Present	Proportion Marked Deer Observed	Population Estimate
10-77	PA-18 Super Cub	B	not recorded	112	3	17	0.177	635
09-78	PA-18 Super Cub	B	not recorded	176	3	16	0.188	939
10-79	PA-18 Super Cub	B	not recorded	278	13	49	0.265	1048
09-80	PA-18 Super Cub	B	not recorded	548	28	60	0.467	1174
09-81	PA-18 Super Cub	B	mixed sun & clouds	677	38	79	0.481	1407
10-82	PA-18 Super Cub	D	sunny	501	29	74	0.392	1278
10-83	PA-18 Super Cub	D	overcast-occasional light rain	721	23	68	0.338	2132
09-84	PA-18 Super Cub	D	not recorded	490	20	57	0.351	1396
10-85	PA-18 Super Cub	D	10-15 cm snow cover-cloudy	398	20	41	0.488	816
10-86	PA-18 Super Cub	D	mostly sunny	397	15	53	0.283	1403

Table 2.3. Population estimates from Lincoln Indexes and final estimates from modeling, including mortality and survival information for the Missouri River Breaks study area, 1977-1987.

Time Period	Total Numbers of Mule Deer								
	Autumn			Winter			Spring		
	Lincoln Index	Modeled Estimate	% Deviation from LI	Lincoln Index	Modeled Estimate	% Deviation from LI	Lincoln Index	Modeled Estimate	Deviation from LI
1977-78	635	675	+0.063	498	520	+0.044	583	450	-0.228
1978-79	939	800	-0.148	751	760	+0.012	573	640	+0.117
1979-80	1048	1135	+0.083	1020	1020	0.000	911	910	-0.001
1980-81	1174	1355	+0.154	1033	1175	+0.138	1084	1080	-0.004
1981-82	1407	1555	+0.066	1307	1215	-0.070	1279	1070	-0.163
1982-83	1278	1490	+0.166	1151	1200	+0.043	1213	1115	-0.081
1983-84	2132	1715	-0.196	1575	1545	-0.019	1157	1180	+0.020
1984-85	1396	1365	-0.022	1136	1135	-0.001	864	870	+0.007
1985-86	816	1075	+0.317	983	975	-0.008	932	915	-0.018
1986-87	1403	1480	+0.055	1401	1355	-0.033	1220	1230	+0.008
			$\lvert \bar{X} \rvert = 0.131$			$\lvert \bar{X} \rvert = 0.037$			$\lvert \bar{X} \rvert = 0.065$

Table 2.4. Mark-recapture population estimates (Lincoln Indexes) for mule deer from aerial surveys on the Missouri River Breaks study area, early winter, 1977-1986.

Date	Aircraft	Pilot	Conditions	Total Deer Observed	Marked Deer Observed	Marked Deer Present	Proportion Marked Deer Observed	Population Estimate
12-77	Helicopter Bell 47G-B2 Soloy	A	25 cm snow cover, mixed sun and clouds, 12° to -18°C	322	11	17	0.647	498
12-78	Helicopter Bell 47G-B2 Soloy	A	15-20 cm snow cover, mostly sunny, -9° to -15°C	501	22	33	0.667	751
12-79	Helicopter Bell 47G-B2 Soloy	A	Bare and dry, mostly sunny, -1° to -7° C	680	30	45	0.667	1020
01-81	Helicopter Bell 47G-B2	B	Bare and dry, -1° to 2° C	854	43	52	0.827	1033
12-81	Helicopter Bell 47G-B2	B	2.5 cm new snow, -12° to -23° C	1062	52	64	0.813	1307
12-82	Helicopter Bell 47G-B2	B	Patchy snow, -4° to 9° C	934	43	53	0.811	1151
12-83	Helicopter Bell 47G-B2	B	15 cm new snow, overcast -7° to -12° C	1225	49	63	0.778	1575
12-84	Helicopter Bell 47G-B2	B	8 cm snow cover, mostly sunny, -9° to -15° C	947	40	48	0.833	1136
12-85	Helicopter Bell 47G-B2	B	20 cm snow cover, mostly sunny, -9° to -23° C	756	30	39	0.769	938
12-86	Helicopter Bell 47G-B2	B	Mostly sunny and bare with patchy snow, -4° to 2° C	957	28	41	0.683	1401

(1983 and 1985). Patchy snow cover (1982 and 1986) may result in more variable observability. The Lincoln and modeled population estimates were very close for early winter (Table 2.3), deviating by an average of 3.7%.

Spring surveys were conducted with a helicopter during 1978-1980 and a Piper SuperCub from 1981 through 1987 (Table 2.5). The SuperCub surveys were generally flown a week or two later than the helicopter surveys, shortly after "green-up" when most deer concentrated on open ridgetops to feed on new growth. Observability from the helicopter was high and similar to early winter except during 1978 when survey conditions were poor, the marked sample was low, and deer were actively moving to their normal ranges from areas along the river where they had concentrated during the severe winter.

Average observability from the SuperCub was also high (68.3%), and the coefficient of variation between years was low (8.0%). Both cloud cover and stage of vegetation "green-up" may influence observability from a fixed-wing aircraft during spring. For example, slightly more than 60% of the marked deer were observed in 1983 and 1986 when skies were generally overcast, and the 1986 survey was conducted before "green-up" was sufficiently advanced for maximum deer use of open areas. Excluding those years, observability averaged 71%. The average deviation between Lincoln and modeled population estimates for spring was 6.5% (Table 2.3).

The accuracy of our counts and percentages of marked deer observed during winter and spring were at least as high and usually higher than reported by others for mule deer (Bartmann et al. 1986), white-tailed deer (Rice and Harder 1977, Floyd et al.1979, Beasom et al. 1986), and moose (LeResche and Rausch 1974). Variation in percentages of marked deer observed during winter and spring among years was much less than reported elsewhere for deer (Bartmann et al. 1986, Beasom et al. 1986), but similar to that for aerial surveys of moose conducted by experienced observers under excellent conditions (LeResche and Rausch 1974).

The high precision of observability indices for winter and spring provided confidence in the accuracy of annual population estimates for those seasons. For example, during 6 of the 7 winter surveys flown with pilot B, the proportion of marked deer observed varied only from 0.77 to 0.83 (Table 2.4). During the seventh year, when survey conditions were poor, observability was 0.68. If we assume a total count of 1,000 deer and apply a mean observability index of 0.80 (52 of 65 marked deer seen), our Lincoln estimate would be 1,250 deer. Considering the possible range in observability recorded for most years, we might expect the total population to lie between 1,200 (1,000/0.833) and 1,300 (1,000/0.769).

Table 2.5. Mark-recapture population estimates (Lincoln Indexes) for mule deer from aerial surveys on the Missouri River Breaks study area, spring, 1978-1987.

Date	Aircraft	Pilot	Conditions	Total Deer Observed	Marked Deer Observed	Marked Deer Present	Proportion Marked Deer Observed	Population Estimate
03-78	Helicopter Bell 47G-B2 Soloy	A	Snow on north slopes, mixed sun and clouds.	255	7	16	0.438	583
03-79	Helicopter Bell 47G-B2	A	Snow on north slopes.	409	35	49	0.714	573
03-80	Helicopter Bell 47G-B2	C	Snow on north slopes.	683	48	64	0.750	911
03-81	PA-18 Super Cub	B	Bare ground, sunny.	747	51	74	0.689	1084
03-82	PA-18 Super Cub	B	Bare ground, sunny.	869	53	78	0.680	1279
03-83	PA-18 Super Cub	B	Overcast, little "green up".	731	44	73	0.603	1213
03-84	PA-18 Super Cub	B	Bare ground, sunny.	855	51	69	0.739	1157
04-85	PA-18 Super Cub	B	Bare ground, sunny.	643	32	43	0.744	864
04-86	PA-18 Super Cub	B & D	Overcast, windy	576	34	55	0.618	932
04-87	PA-18 Super Cub	B	Mixed sun and clouds.	861	24	34	0.706	1220

For greater certainty, or if survey conditions were poor, we could extend the upper limit expected to 1,464 (1,000/0.683). For most winter and spring surveys, the true total population probably fell within a narrower range of deviation from the Lincoln estimate than would be indicated by standard confidence intervals (Overton and Davis 1969) about the estimate.

In the example given above, with a Lincoln estimate of 1,250 deer, a 95% confidence interval estimated a possible range in total numbers from 948 to 1,648. Both extremes were unlikely. During all early winter surveys and half of those in spring, the lower confidence estimate was below the number of deer actually counted. Similarly, during most census intervals, it was biologically and mathematically impossible for deer numbers to increase from the lower limit calculated for one period to the upper limit for the next (or vice versa) when concurrent information on natality and mortality within the population were considered. Those data reduced the practical confidence interval to well within the standard 95% limits. Because population estimates were made 3-4 times each year with data on natality, mortality, and population composition available, we are confident that "true" population levels deviated within a very narrow range from the Lincoln estimate. Arithmetic modeling indicated the likely direction and degree of that deviation as provided by our ultimate, modeled population estimate (Appendix A).

During years in which marked deer were available for calculation of Lincoln indices, population trend and relative annual changes in numbers were similar whether the Lincoln estimates, the modeled estimates, or the actual counts were used (Fig. 2.1). Thus, conclusions about population dynamics would not be altered even if the precision of individual estimates is questioned.

Findings and methods developed during 1976-1987 enabled us to refine previous early winter population estimates (Mackie 1970, 1973, 1976) and construct models that estimated autumn and spring populations on the study area each year from 1960 through 1975. Initial estimates for 1960-1963 were developed by plotting numbers of mule deer observed by location on gridded aerial photographs and from aerial surveys during winter (Mackie 1970). Those for 1964-1975 were developed by applying general observability indices ranging from 60 to 70% (ave. 65%) (Mackie 1976) to numbers of deer counted in helicopter surveys in early winter to calculate relative densities within areas surveyed each year. Total populations were calculated by extrapolating densities on areas surveyed to the entire area. Arithmetic modeling accounted for natality and known or estimated mortality and reconciled sex and age composition between successive

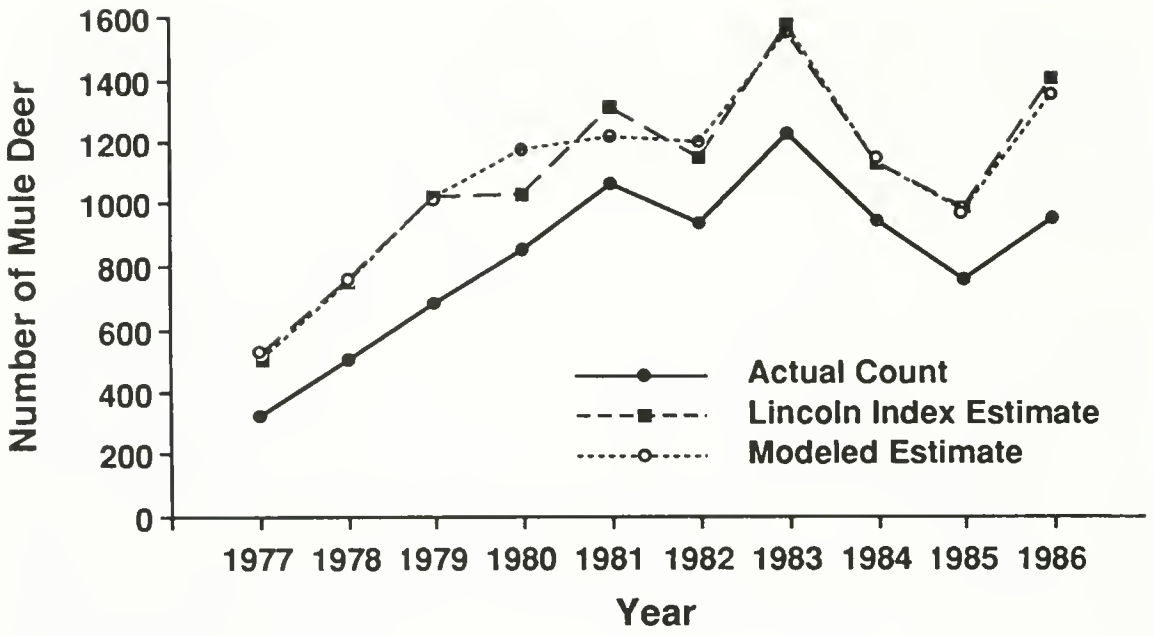


Figure 2.1. A comparison of the actual count of mule deer during early winter helicopter surveys with the Lincoln Index estimate and the modeled estimate, 1977-1986.

estimates. Modeling was also employed to calculate estimated size and composition during years of partial or incomplete aerial surveys and for 1968 when no survey was made.

Population estimates for 1973-1975 were refined by applying the average observability index for 1977-1979 (66.0%) to early winter counts. Surveys during both periods were flown by the same pilot (A) and principal observer (Mackie) and were of equal coverage and intensity. Fawn survival and known adult mortality on the study area and the adjacent NCRCA research area (Knowles 1975, 1976) were also considered. Estimates for earlier years when complete surveys were also flown by Mackie and pilot A (1964, 1965, 1970, and 1971) were based on a 60% observability factor because they were not flown for as close or complete coverage of the study area as those during 1973-1987. Estimates initially derived from partial or no surveys during 1960-1963 (Mackie 1970) and 1966-1969 were refined after comparison with estimates from full surveys before and after years of partial surveys. Additional data for modeling population size and composition were available from helicopter surveys covering portions of the study area in 1963, 1966, 1967, and 1972, a fixed-wing survey in 1969, and from classifications along vehicle routes through the area during autumn, winter, and spring 1960-1963. The partial survey flights also provided a minimum count of deer

and general impressions about population size relative to prior and subsequent full-coverage surveys. Sex and age classifications on the NCRCA and adjacent areas were available for many of these years, including 1968 when no data were obtained on our study area. Harvest statistics, available for the hunting district which included our study area, provided information on relative hunting losses. Additionally, Mackie monitored harvests on the study area during 1960-1965.

Because population estimates for 1960 through 1975 were more dependent on modeling, they may be less accurate than estimates for 1976-1987. Considering all evidence, however, they must be close to actual population levels. For example, one question might relate to estimates from 1966 through 1969, when neither census nor complete classification surveys were conducted. Complete surveys earlier (1964 and 1965) and later (1970 and 1971) provided reasonably accurate population estimates and a measure of trend through intervening years. Data from the incomplete helicopter survey in early winter 1966 indicated little change in population size from the 725 estimated for 1965, whereas data from the partial survey in 1967 indicated an increase that year. Also, fawn survival was much better during 1967 than 1966 and harvest questionnaires revealed that hunting loss was lower. Fawn:doe ratios obtained for mule deer in adjacent areas north of the Missouri River in 1968 indicated continuing high fawn survival and a further increase in population size through early winter that year. Some mortality likely occurred during the relatively severe winter of 1968-69. However, the population must have continued to increase through early winter 1969, when fawn production and survival remained quite high, if the estimated number of about 1,290 was to be reached in early winter 1970. Arithmetic modeling, given available data on fawn survival to December, relative levels of hunting mortality reported by questionnaire, and weather patterns, indicated a relatively narrow range of possible population levels for the four years. Although actual populations for each of the 3 periods for which estimates were made each year could have deviated from our estimates (Appendix Table A), the deviation would not have been sufficient to influence major conclusions concerning population dynamics.

CHAPTER 3

CHARACTERISTICS OF THE STUDY AREA

Location and Physiography

The Missouri River Breaks comprise a 10 to 50-km-wide by 300 km-long belt of rugged badlands along the Missouri River and its tributaries in northcentral Montana. Distinguished from adjacent rolling plains by physiographic and vegetative characteristics, the "breaks" have long been recognized to provide superior habitat for mule deer within the Missouri Plateau Region of the northern Great Plains.

Our study was conducted primarily within a representative, 275 km^2 area located at 47°30' north latitude, 108°30' west longitude, approximately 40 km northeast of Roy, in central Montana (Figs. 3.1 and 3.2). The area extends about 30 km east from U.S. Highway 191 and 7-11 km south from the Missouri River. It encompasses two major drainages, Sand Creek and Carroll Coulee, that dissect the area in a dendritic pattern and become progressively wider, deeper, and steeply sloped as they approach the river (Fig. 3.3). Close interspersion of sharply-cut drainageways or "coulees" and open ridges that extend onto the area from adjacent plains provides the characteristic badlands or breaks topography (Fig. 3.4).

The entire area slopes gently to the north and east. Elevations range from about 945 m along the southern edge of the area to about 685 m on the Missouri River floodplain. The greatest relief over the shortest distance occurs near the river on the northern portion of the area. Rolling plains extend, with slightly increasing elevation, to the south and southwest.

Soils of the area are derived primarily from the Bearpaw Shale Formation and are predominantly heavy clay loams of the Lismas-Thebo series, with moderate amounts of salts. Shallow layers of glacial till occur on the highest level ridgetops. These soils are relatively impermeable to water and runoff is high. Extensive natural erosion is characteristic, especially on steep sparsely vegetated slopes, where underlying shales are exposed, and along ephemeral streamcourses. The soils are considered too shallow, too heavy and plastic, and generally too steep for cultivation (Gieseker et al. 1953).

The Missouri River provides permanent water along the northern boundary of the study area. Sand Creek and Carroll Coulee are intermittent streams which flow only during spring runoff or following heavy rains. There are 62 man-made stockwater impoundments and 4 wells, developed to provide

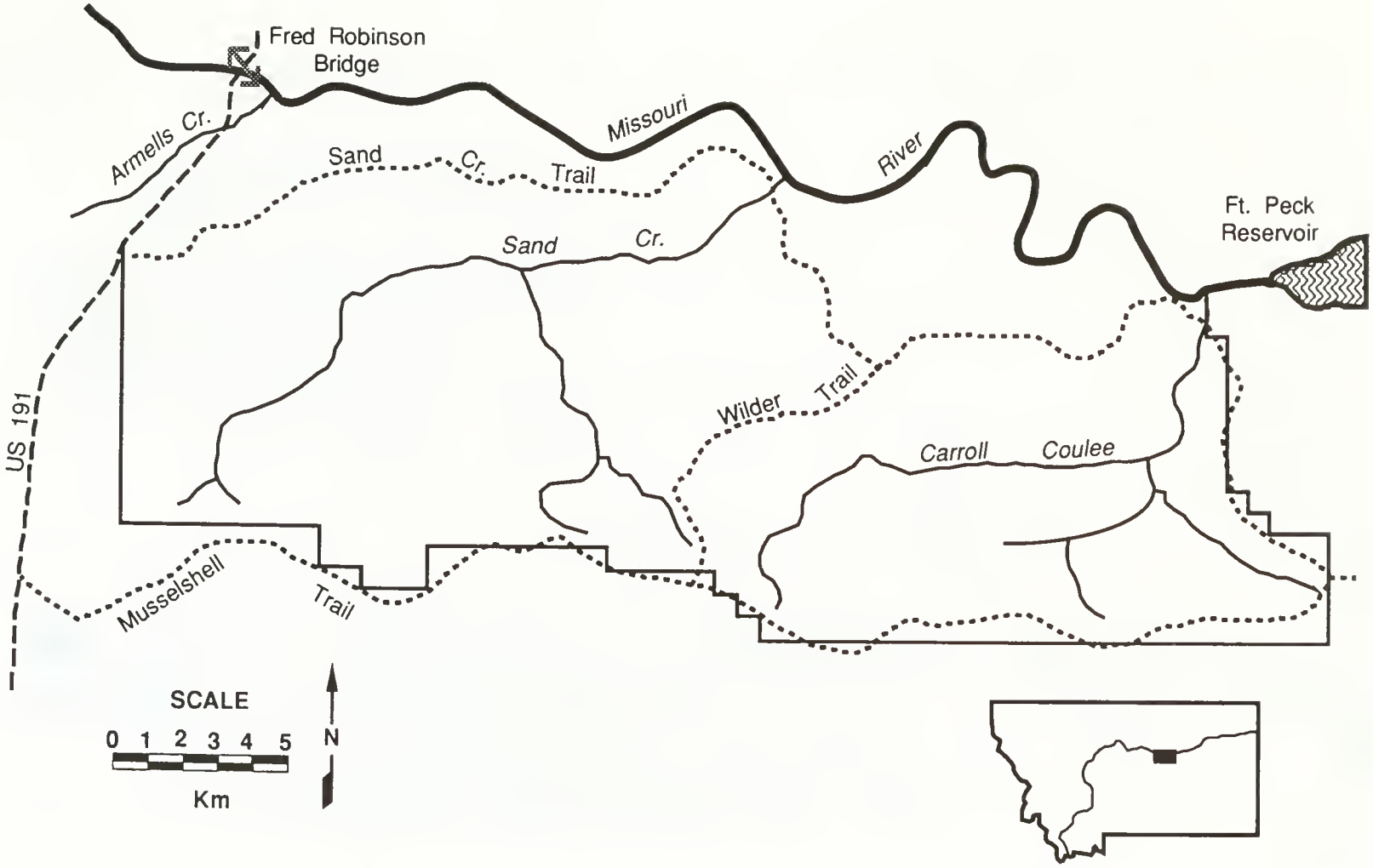


Figure 3.1. Map of study area showing location and major features.

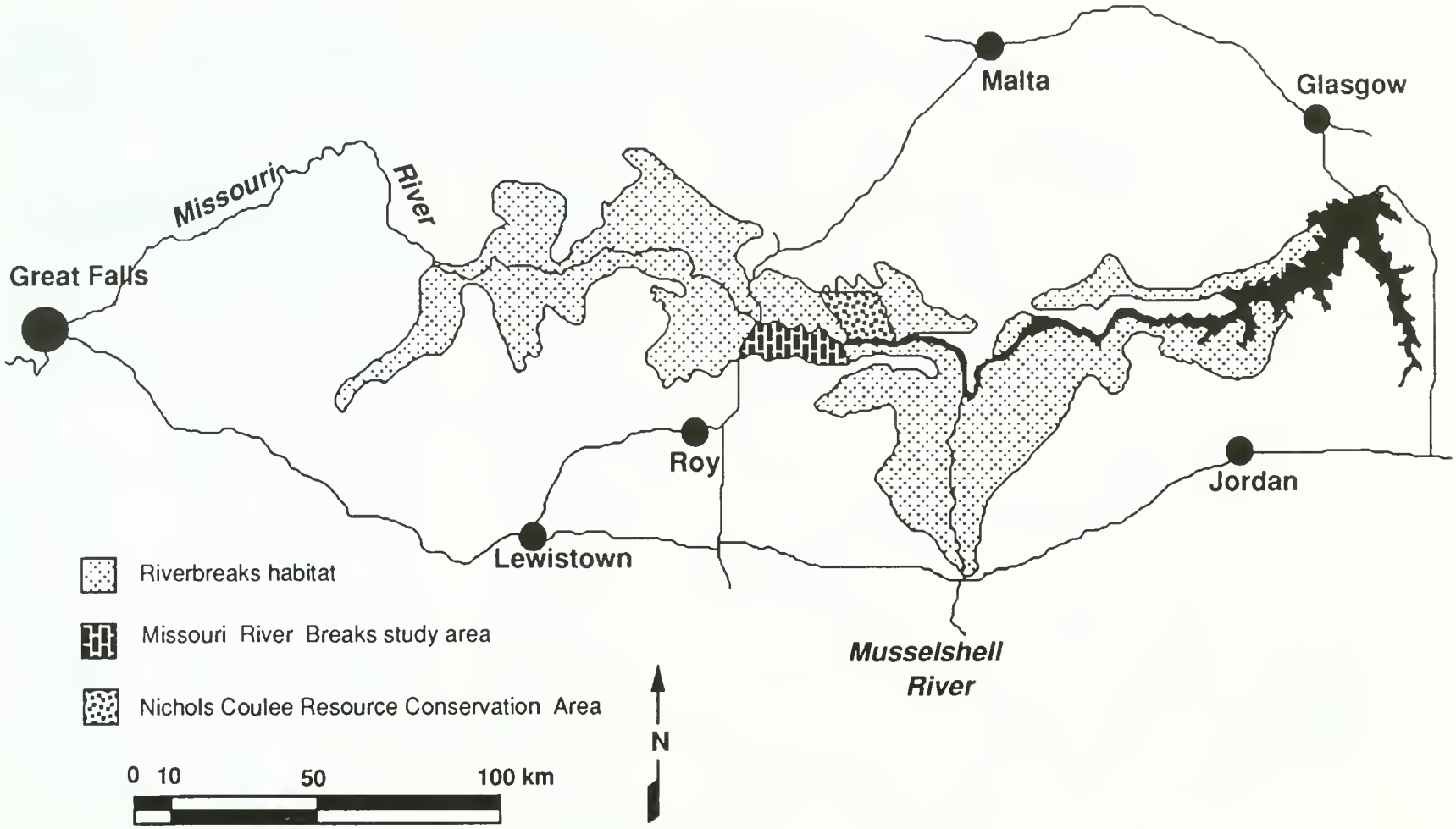
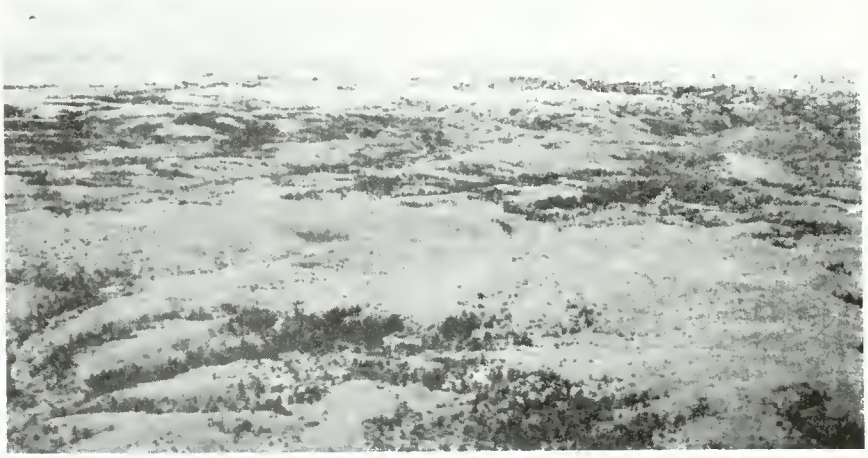


Figure 3.2. A map showing the extent of the riverbreaks habitat, the location of the study areas, major towns, highways, and rivers.

Figure 3.3. Aerial photo masaic of the study area.

A



B

C

Figure 3.4. Aerial views of the study area showing (A) drainage head areas, (B) mid-level drainage areas, and (C) steeper terrain near the Missouri River.

additional permanent sources of stockwater, on the area. Nearly all of the reservoirs were small (< 1 ha) and more than one-third were dry by late summer in average water years. During the driest years only 28 contained water, mostly in small amounts and of low quality. Three of the 4 wells were developed during the last 2 years of the study to supply watering tanks at various sites on the south-central portion of the area. During years or periods of above-average precipitation, water is also available in natural depressions throughout the area.

Access is provided by a paved highway (U.S. 191) along the western boundary, several unpaved "roads" extending through the area from the highway, and numerous vehicle "trails" along ridgetops. All unpaved roads and trails are impassable when wet.

Climate

The climate is semiarid, characterized by moderately low and variable precipitation, low relative humidity, moderate to strong winds, and great extremes in temperature.

Records for the U.S. Department of Commerce weather station, Roy 8 NE, located approximately 25 km southwest of the center of the study area show a 42-year (1943-1985) mean annual temperature of 6.5 C (range 4.3 - 8.3 C, CV = 4%). January is the coldest month (Fig. 3.5), with an average temperature of -8.4 C, while July is the warmest (20.8 C). Mean annual (1939-1985) precipitation is 35.4 cm (range 17.9 - 63.9 cm, CV= 27%), most of which occurs as rain during spring and summer (Fig. 3.5). Precipitation is normally highest during June (7.5 cm) and lowest during February (1.0 cm). Total snowfall ranged from 0.2 m to 2.2 m. Snow depths exceeding 0.3 m are rare, though occasionally accumulations up to 0.9 m persist for significant periods of time (e.g. 1977-78 and 1978-79). Warm, southwesterly "chinook" winds occur periodically during many winters to moderate temperatures and reduce snow accumulations. The average frost-free season is 128 days, but the effective growing season is shorter, usually extending only from mid-April through the end of June.

Trends in annual temperature, growing season and annual precipitation, and winter snowfall and severity (Figs. 3.6 and 3.7) illustrate the marked seasonal, annual, and periodic fluctuations that characterize the climate and weather conditions on the area. Long-term (1580-1980) trends in moisture were calculated as a relative moisture index from tree-ring data for Douglas fir (*Pseudotsuga menziesii*) on the study area by the University of Arizona Tree Ring Laboratory (D. Meko and C. Stockton, pers. commun., Fig. 3.8). These

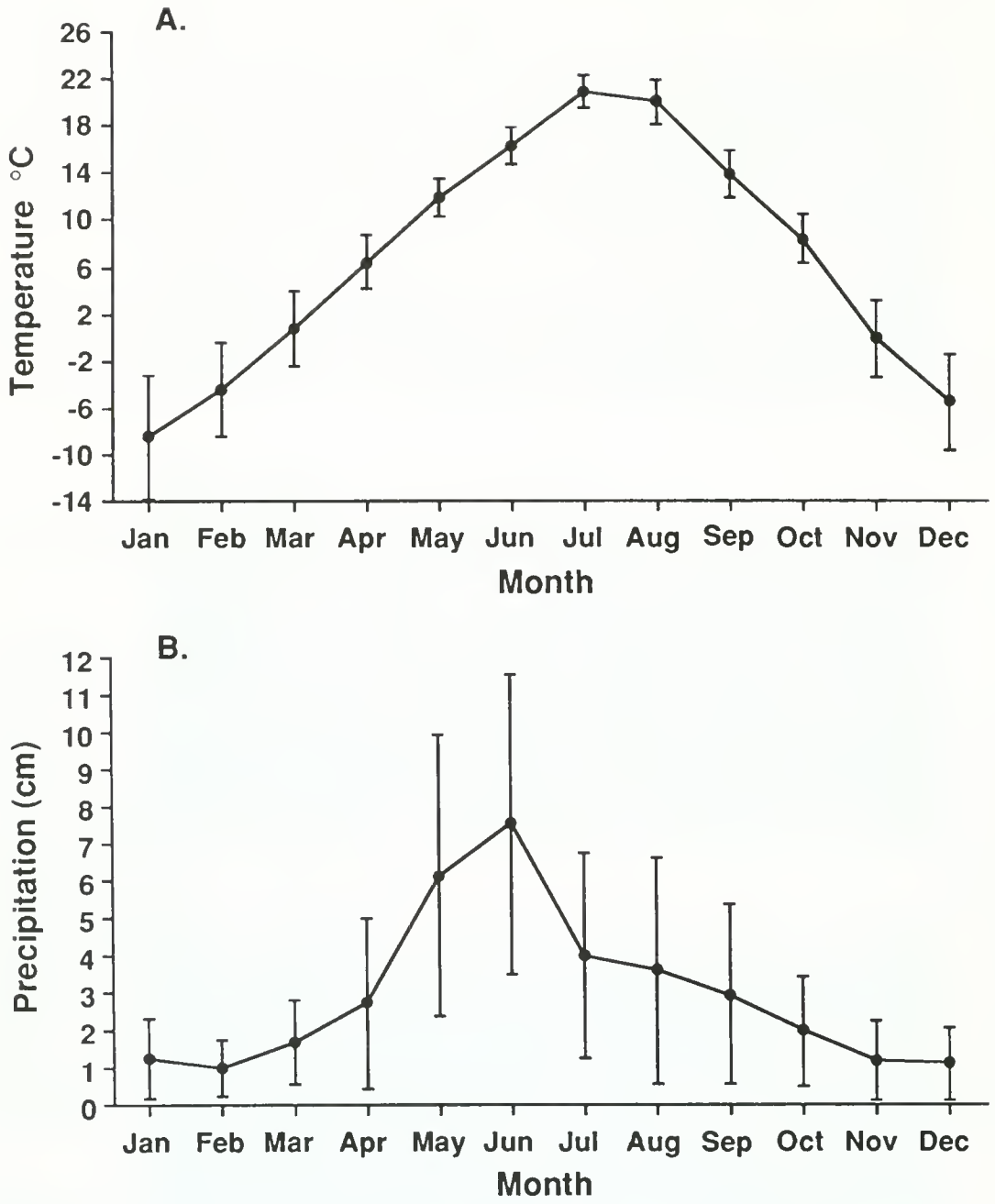


Figure 3.5. A. Forty-two year (1943-1985) mean and standard deviation of monthly temperatures at Roy 8NE weather station. B. Forty-seven year (1939-1985) mean and standard deviation of monthly precipitation at Roy 8NE weather station.

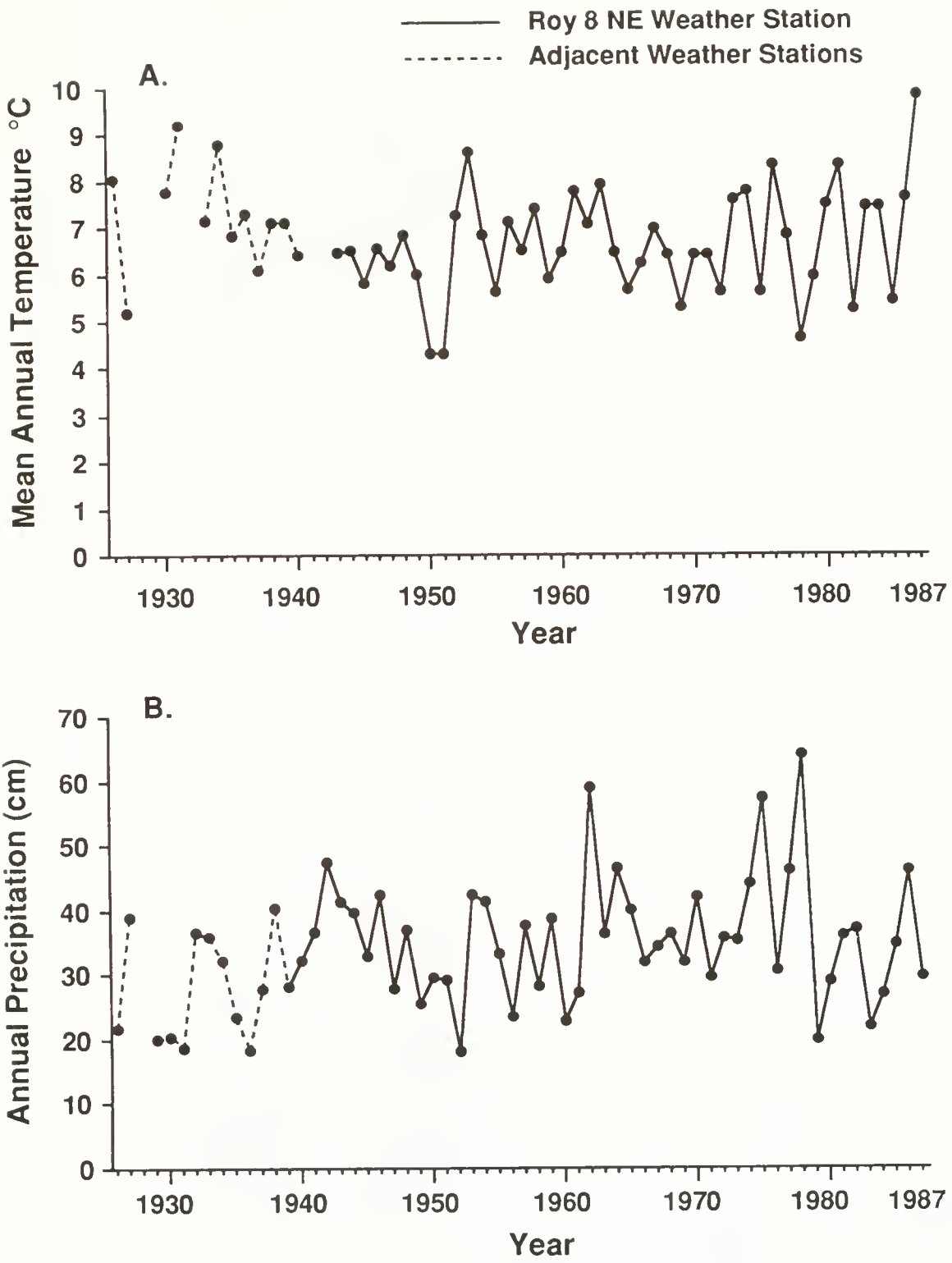


Figure 3.6. Mean annual temperature (A) and precipitation (B) at the Roy 8NE weather station (or adjacent stations prior to 1940) for 1926 through 1987.

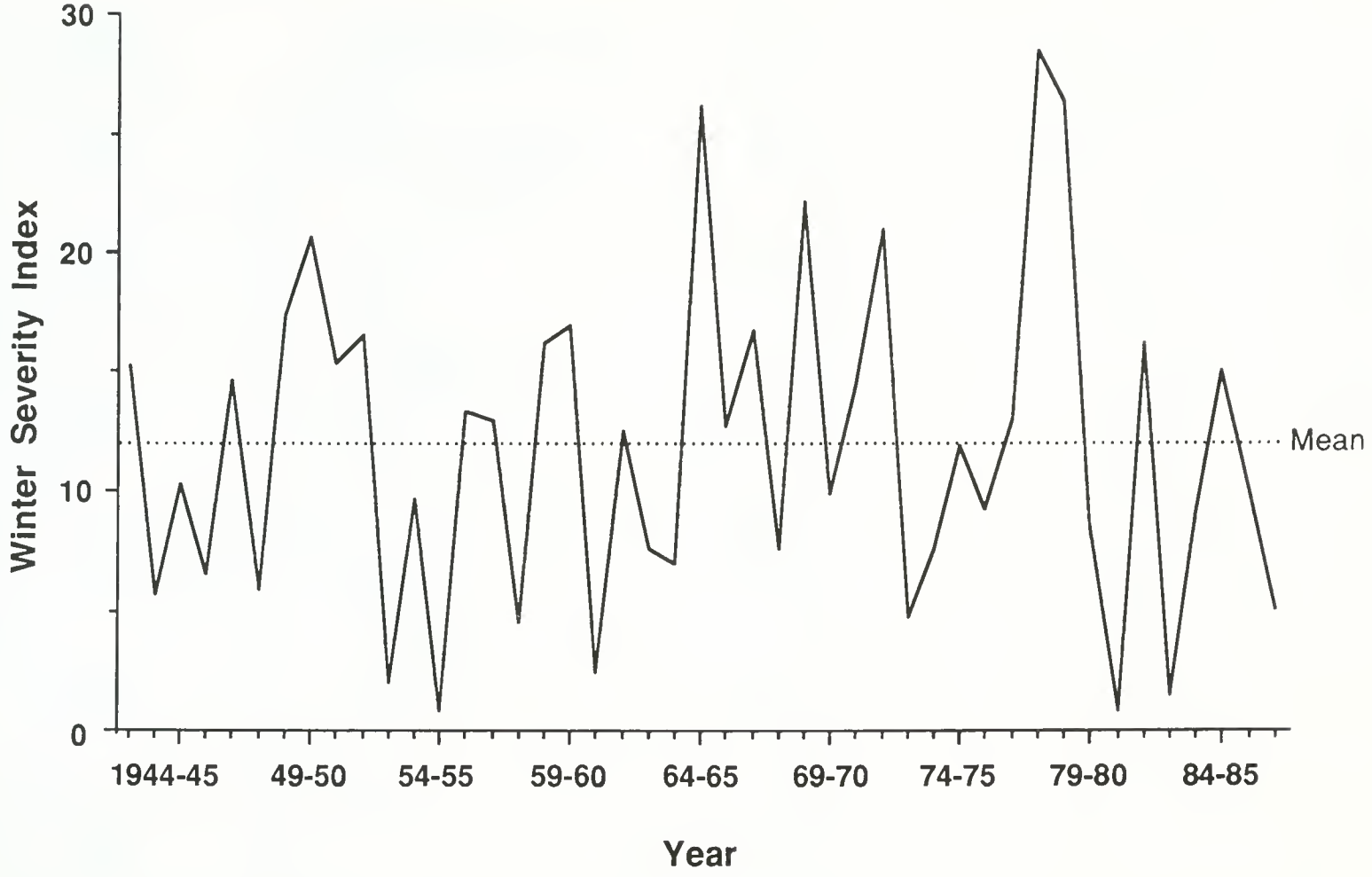


Figure 3.7. A relative winter severity index (see Chapter 2) calculated for 1942-43 through 1986-87.

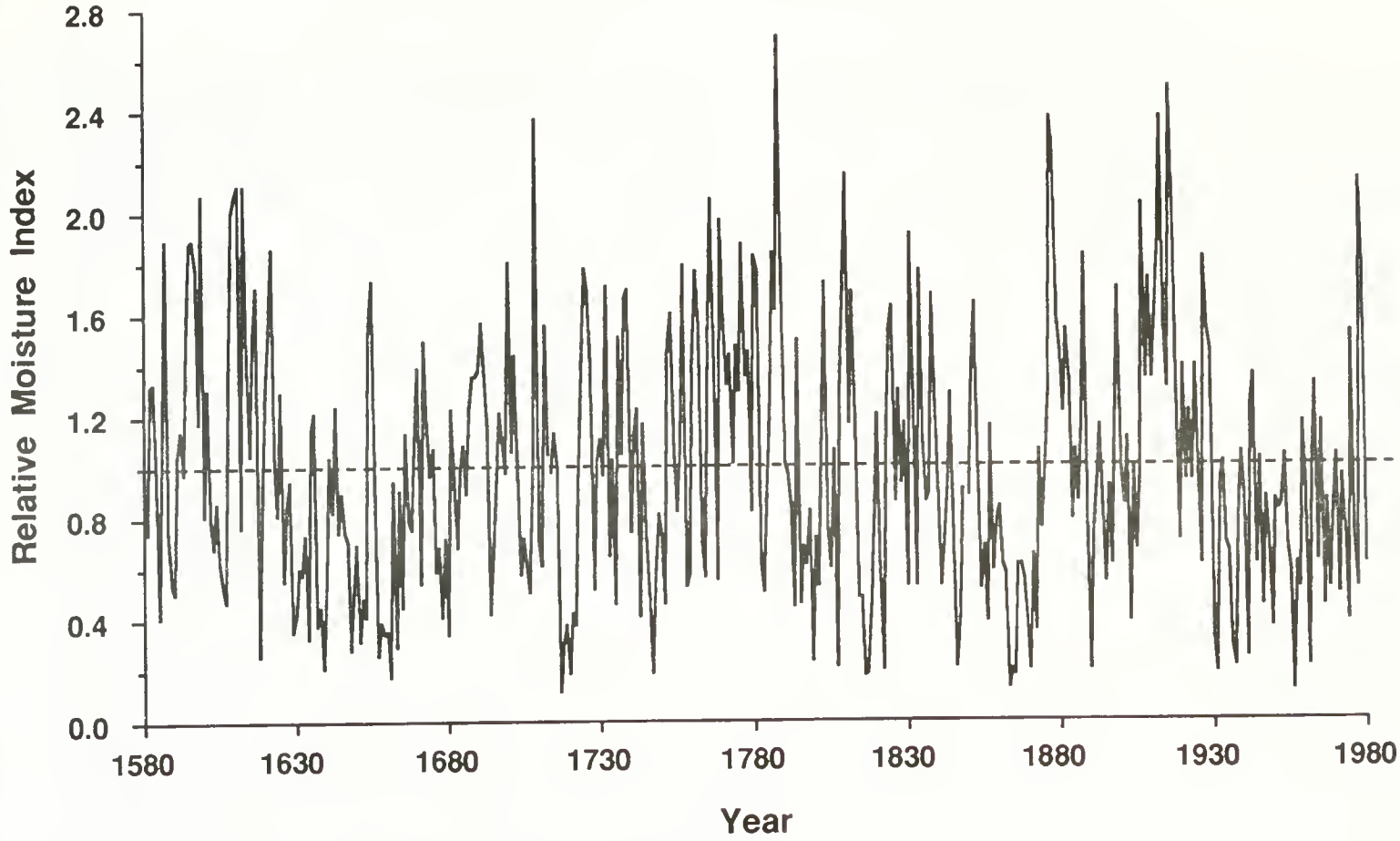


Figure 3.8. Relative moisture index for the study area for years 1580 through 1980 calculated from Douglas fir growth ring data (with permission from C. Stockton and D. Meko, Tree Ring Laboratory, University of Arizona, Tucson).

trends provided further documentation of the fluctuations and opportunity to relate recent conditions to those of the past. From this perspective, the nature and range of fluctuations observed during our study are consistent with, and fall within, those of the past; periods of drought interspersed with periods of high moisture are the rule. Overall, however, the period 1930 to present has been one of relative drought matched only by a period from about 1625 to 1685.

Vegetation

The varied topography and soils support a complex mosaic of vegetation. Mackie (1970) recognized 8 major vegetation/habitat types comprising 12 communities (associations or associes) occurring on uplands. Two additional types characterized bottom- lands along the Missouri River. Our classification (Table 3.1) was similar with respect to major types, described herein as vegetation-physiographic types, but we also delineated "cover types" based on degree of overhead cover and fire history in forested habitats. This approach describes communities in terms of existing vegetational characteristics and seral stage rather than potential or climax vegetation.

Forested types covered approximately 51% of the area, and generally occurred as scattered, open, and medium-density stands of coniferous trees and shrubs along side-slopes of drainages (Table 3.1). Dense stands, characterized by almost continuous contact between individual tree canopies of relatively small (narrow) and similar size, did not occur. Medium density stands were those in which almost all canopies were in contact and the individual tree canopies were relatively large but included a variety of sizes. Open stands held trees of sufficient density to provide frequent contact between canopies, but also contained numerous openings. Scattered stands were those in which individual trees were widely separated with few if any canopies in contact. Riparian forest, dominated by deciduous trees and shrubs, was restricted to Missouri River bottomlands (2.5% of the area).

Low shrub and grass dominated communities covered 49% of the area, including all ridgetops, coulee bottoms, benches, and some steep, south-facing slopes. Extensive interspersion of forest and open types provides a general savannah-like aspect to the vegetation (Figs. 3.3 and 3.4). This aspect is accentuated by the prevalence of scattered and open cover types in forested communities (Table 3.1) and the generally low stature of coniferous trees, which rarely exceed 15 m in height.

Detailed descriptions of the major vegetation/habitat types on the study area are provided by Mackie (1970). The

Table 3.1. Relative occurrence of vegetation and cover types on the Missouri River Breaks study area.

Vegetation Type	Cover Type	Number of Hectares	% of Study Area
Sagebrush Grassland		10,328	37.7
Pine-Juniper-Grass	medium density	937	3.4
	open	2,498	9.1
	scattered	1,610	5.9
	burned	61	0.2
	Total	5,106	18.6
Pine-Juniper Shale	medium	90	0.3
	open	2,491	9.1
	scattered	1,443	5.3
	Total	4,024	14.7
Douglas Fir-Juniper	medium	1,398	5.1
	open	946	3.5
	scattered	344	1.3
	burned	903	3.3
	Total	3,591	13.1
Grassland Bottoms		1,058	3.9
Greasewood		1,040	3.8
Shale-Longleaf Sage		756	2.8
Pine-Juniper-Fir	medium	291	1.1
	open	281	1.0
	scattered	10	tr.
	burned	127	0.5
	Total	709	2.6
River Riparian		676	2.5
Silver Sagebrush		112	0.4
TOTAL		27,400	

following descriptions summarize the extent of occurrence, general physiographic relationships, and more important vegetational characteristics of each. Frequencies of occurrence of important shrub species, total grasses, and total forbs in 6 types covering 91% of the study area are listed in Table 3.2. The relative abundance of forbs eaten by deer in those types during May, July, and September is shown in Table 3.3.

Sagebrush-grassland (*Artemisia-Agropyron*) covers approximately 38% of the area and is usually restricted to level or gently rolling ridgetops and plains. Big sagebrush (*Artemisia tridentata*), which averages about 0-20% canopy coverage, is the principal shrub. Minor shrubs include greasewood (*Sarcobatus vermiculatus*), Arkansas rose (*Rosa arkansana*), and rubber rabbitbrush (*Chrysothamnus nauseosus*). Western wheatgrass (*Agropyron smithii*) and bluebunch wheatgrass (*A. spicatum*) predominate among grasses, which provide the greatest amount of ground cover (40-80% canopy coverage). The forb component varies widely by season and year, with mean canopy coverage of 5-20%.

The **pine-juniper-grass** (*Pinus-Juniperus-Agropyron*) type covers approximately 19% of the study area, occurring on sites ranging from slight slopes bordering sagebrush-grassland to moderately steep slopes. Stands on slight slopes often have low densities of pine and good grass cover (Table 3.2). Those on steeper sites with north, east, and west exposures usually have greater coverage of pine, less grass, and a well-developed understory of juniper. Overall, grass coverage is less and shrub coverage greater than on the sagebrush-grassland type. Snowberry (*Symporocarpus* spp.), rose (*Rosa* spp.), fragrant sumac (*Rhus aromatica*), and Rocky Mountain juniper (*J. scopulorum*) are major shrubs. Forbs are abundant and include a greater variety of species than any other type on the area.

The **pine-juniper-shale** (*Pinus-Juniperus*-Shale) type is largely limited to shale outcroppings on steeper south-facing slopes covering about 15% of the study area. It occurs primarily as scattered and open density stands of ponderosa pine with an understory of Rocky Mountain juniper. Most other shrubs as well as grasses and forbs occur in very minor amounts.

The **Douglas fir-juniper** (*Psuedotsuga-Juniperus*) type covers north-facing slopes and other cool, moist sites comprising about 13% of the area. The best developed and most extensive stands occur within the Sand Creek drainage. Douglas fir dominates the typically open to medium-density overstory. The shrub layer is well developed and dominated by Rocky Mountain juniper, although snowberry, rose, chokecherry

Table 3.2. Percent frequency of occurrence of shrubs, grasses, and forbs within 300 2X5 dm plots in six vegetation types.

Species	AA[a]	PJG	PJS	DFJ	GW & SA
Artemisia cana		0.3	0.3		
Artemisia tridentata	45.7	3.0	0.7	0.7	2.3
Artemisia longifolia		0.7			6.0
Atriplex nutalii					0.3
Chrysothamnus nauseosus	0.3	1.0			
Chrysothamnus viscidiflorus	0.3	0.3		0.3	
Juniperus scopulorum		5.3	17.3	57.0	0.3
Prunus virginiana		1.3		12.3	
Rhus aromatica		9.0	1.0	9.0	
Ribes spp.			0.3	6.7	
Rosa spp.	0.7	27.3	0.3	19.7	0.7
Sarcobatus vermiculatus	0.7				38.6
Symphorocarpos spp.		18.3	0.7	50.3	
Grasses	100.0	76.7	36.7	51.7	35.0
Forbs	72.7	56.3	10.3	47.7	29.7

[a] AA=Sagebrush-grassland, PJG=pine-juniper-grass, PJS=pine-juniper-shale, DFJ=Douglas fir-juniper, GW=greasewood, and SA=shale-longleaf sage

Table 3.3. Number of green forbs per ha in six vegetation types during May, July, and September[a].

	Vegetation Type					
	AA[b]	PJG	PJS	DFJ	GW & SA	Average
May	692,000	99,000	12,000	60,000	50,000	182,600
July	295,000	97,000	2,000	119,000	30,000	108,600
September	14,000	14,000	10,000	45,000	2,000	17,000
Summer Ave.	333,667	70,000	8,000	74,667	27,333	102,733

[a] Includes only those forbs remaining succulent and known to be eaten by mule deer. Yellow sweetclover, for which abundance is extremely variable among years, was excluded.

[b] AA=sagebrush-grassland, PJG=pine-juniper-grass, PJS=pine-juniper-shale, DFJ=Douglas fir-juniper, GW=greasewood, and SA=shale-longleaf sage

(*Prunus virginiana*), aromatic sumac, gooseberry (*Ribes setosum*), and currants (*Ribes* spp.) also are well represented. Overall shrub coverage is greater than in any other type, and only the pine-juniper-grass type has a greater variety of shrubs. Grasses and forbs are relatively sparse, except on burned sites where juniper is reduced and other species, especially grasses, achieve greater importance (Eichorn and Watts 1984).

The **pine-juniper-fir** (*Pinus-Juniperus-Psuedotsuga*) type occurs on sites similar to the Douglas fir-juniper type. It covers about 3% of the area, primarily in the eastern portion. Ponderosa pine is dominant both in the overstory and in regeneration and Douglas fir is relatively limited in abundance. Characteristics of the shrub and herb layers appear intermediate between the Douglas fir-juniper and pine-juniper-grass types.

The **greasewood** (*Sarcobatus*) type covers about 4% of the area. It occurs mainly on higher and drier portions of floodplains and footslopes along the Missouri River and on benches along the lower portions of major drainages. Vegetation is sparse and dominated by greasewood and western wheatgrass.

The **shale-longleaf sage** (Shale-*Artemisia longifolia*) type is vegetationally similar to the greasewood type except for its occurrence on steep shale slopes and the typical dominance of longleaf sage. Eriogonum (*E. multiceps*), a half- shrub, is also more prominent, and greasewood is reduced in importance. The type is of very minor extent, occurring on less than 3% of the area.

The **grassland bottoms** type is found in the upper portions of major drainages as well as on bottoms of second and third order drainages that collectively comprise about 4% of the area. Grasses predominate, but snowberry and rose provide an important shrub component.

The **silver sagebrush** (*Artemisia cana*) type is very minor and occurs primarily on bottoms near the mouth of major drainages. Silver sagebrush and green rabbitbrush (*Chrysothamnus viscidiflorus*)dominate, but grasses, primarily western wheatgrass, are well represented.

The **river riparian** type collectively describes riparian forest and shrub vegetation that occurs along Missouri River bottomlands. Plains cottonwood (*Populus sargentii*), willows (*Salix* spp.), snowberry, and rose are the dominant plant species.

Forage Plant Production, Abundance, Vigor, and Use

Forage Production

The characteristically wide fluctuations in weather-climatic conditions on the study area were reflected in wide variation in plant species production, abundance, and quality, within and among years. Measurements of standing current growth of forbs, grasses, and shrubs during July, 1976-1986 (Table 3.4), show that annual production of forbs on 2 sites within the sagebrush-grassland type varied nearly 16-fold between low and high years, while production of grasses varied by a factor of about 4.5. Current annual growth production of 3 shrub species in the Douglas fir-juniper type varied 5.3-fold between years of high and low production within a shorter, 7-year period that did not include the year of lowest forb growth. Annual production of yellow sweet-clover, a biennial forb highly preferred as forage by mule deer varied even more than forbs in general (Table 3.5).

To further evaluate fluctuations in forage production and estimate annual production and trends for years prior to 1976, a series of regressions relating production to climatic factors were computed. Factors included as independent variables were based on studies by Rogler and Haas (1947), Blaisdell (1958), Dahl (1963), Shiflet and Dietz (1974), Cable (1975), and Smoliak (1986). Ideally, available soil moisture, precipitation during the growing season, and evapotranspiration data were most likely to relate to forage production. Lacking direct measurements of available soil moisture and evapotranspiration for the study area, precipitation prior to and during the growing season and temperature during the growing season seemed to best predict forage production (Blaisdell 1958, and Smoliak 1986). Precipitation prior to and during the growing season influenced available soil moisture, and temperature during the growing season influenced evapotranspiration.

Precipitation and temperature variables most closely correlated with production on the area are listed in Table 3.6. Many combinations of precipitation prior to and during the growing season (including some not listed in Table 3.6) provided high positive correlations with forb and shrub production. Precipitation during April and May was the only variable that provided a significant correlation with yield of grasses. Mean monthly temperature during the growing season was significantly negatively correlated with forb yield and a combined forb-shrub yield index.

Cooler temperatures during April and May might be expected to correlate with higher precipitation during the

Table 3.4. Production (kg/ha) of forbs, grasses, and shrubs on the study area, 1976-1986.[a]

	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	Maximum difference low to high
Total Forbs	121	125	281	376	111	172	236	195	54	24	146	15.7
Grasses	381	256	801	363	215	454	751	403	338	257	957	4.5
3 Shrubs[b]	74	45	237	207	50	101	95	--	--	--	--	5.3
4 Shrubs[c]	--	67	272	283	71	128	138	--	--	--	--	4.2

[a] Forbs and grasses were clipped at 2 sites in sagebrush-grassland type, shrubs were clipped at 2 other sites in Douglas fir-juniper type. Data represent the average for the 2 sites for each category.

[b] Fragrant sumac, rose, and snowberry.

[c] As above and chokecherry.

Table 3.5. Abundance (number of plants/% frequency) of yellow sweetclover in 310 4x10 dm plots on 31 sites, 1977-1986.

Year	First Year Plants	Second Year Plants	Avg. Weight[a] (g) per plant	kg/ha
1977	11/1.9	0/0		<0.05
1978	3227/44.2	21/3.5	1.35	354
1979	0/0	1407/38.1	6.70	760
1980	90/3.5	0/0	0.06	0.4
1981	2582/54.2	9/2.9	0.06	12.5
1982	2563/53.9	291/26.5	0.34	78
1983	544/22.9	769/46.8	0.66	70
1984	3205/35.5	21/3.2	0.04	10.4
1985	46/3.2	0/0	0.02	0.07
1986	3695/62.6	108/11.9	0.71	218

[a] Average weight (g) per plant taken from separate clipped plots.

same period. Although this often was the case, cool temperatures also occurred in the absence of precipitation. Thus, mean temperature for April and May was significantly negatively correlated with forb production, but precipitation during those months was not (Table 3.6). The negative relationship between mean growing season temperature and forage production appeared to be independent of a correlation with precipitation.

Multiple regression models incorporating both temperature and precipitation variables were computed for the period 1976-1982, when production of all forage classes was measured (Table 3.7). Mean temperature during May and precipitation during the previous July-April period together explained 91.5% of the annual variation in forb yield ($R^2 = 0.915$, $F = 21.55$, $P = 0.009$). Stepwise procedures indicated that both variables were significantly related to forb yield; mean May temperature explained 73% of the variation and an additional 18.5% was explained by July-April precipitation. Production of 3 shrub species was best predicted by precipitation during July-May

Table 3.6. Simple correlation coefficients for forb, shrub, and grass yield (kg/ha) versus various precipitation and temperature variables, 1976-1982.

Independent Variables	Dependent Variables: Forb Yield	Shrub Yield (3 species)	Forb & shrub Yield	Shrubs[a] Yield (4 species)	Grass Yield
July-March precipitation[b]	0.729	0.779*[c]	0.773*	0.892*	0.393
July-May precipitation	0.783*	0.892**	0.855*	0.906*	0.634
Sept.-May precipitation	0.802*	0.875**	0.859*	0.849*	0.701
Sept.-April precipitation	0.854*	0.852*	0.879**	0.884*	0.413
July-April precipitation	0.755*	0.810*	0.802*	0.926**	0.383
April-May precipitation	0.458	0.649	0.558	0.533	0.859*
April-May mean temperature	-0.907**	-0.672	-0.828*	-0.736	-0.589
May mean temperature	-0.854*	-0.636	-0.782*	-0.705	-0.594

[a] Yield for 4 species of shrubs measured only during 6 years, 1977-1982.

[b] Precipitation data are from months prior to and during the growing season. Temperature data are during the growing season.

[c] * Significant at $P < 0.05$
** Significant at $P < 0.01$.

Table 3.7. Multiple correlation coefficients (R^2) of forb and shrub yield (kg/ha) with various precipitation and temperature variables, 1976-1982.

Independent Variables	Dependent Variables: Forb Yield	Shrub Yield (3 species)	Forb & Shrub Yield	Shrub[a] Yield (4 species)
July-March precipitation[b] and April-May mean temperature	0.887**[c]	0.682	0.818*	0.820
July-May precipitation and April-May mean temperature	0.888**	0.810*	0.861*	0.845
September-May precipitation and April-May mean temperature	0.872*	0.771*	0.833*	0.769
September-April precipitation and May mean temperature	0.902**	0.746	0.864*	0.801
July-April precipitation and May mean temperature	0.915**	0.758	0.878*	0.868*

[a] Yield for 4 species of shrubs measured only during 6 years, 1977-1982.

[b] Precipitation data are from months prior to and during the growing season. Temperature data are during the growing season.

[c] * Significant at $P < 0.05$
** Significant at $P < 0.01$.

(R^2 = 0.795, F = 19.4, P = 0.008). Temperature variables did not significantly (P > 0.25) add to the predictive power of regressions on shrub yield. However, a combined index of forb and shrub production was most significantly related to a combination of precipitation from July through April and mean temperature for May (R^2 = 0.878, F = 14.43, P = 0.017). Stepwise procedures indicated that the precipitation factor contributed most to the regression (R^2 = 0.643, F = 9.02, P = 0.03), but mean May temperature also contributed significantly (R^2 = 0.235, F = 7.72, P = 0.05).

Production measurements were limited to forbs and grasses after 1982. Addition of those data to the regression model did not significantly alter results. Precipitation during April and May continued to be significantly positively correlated with grass production (r = 0.863), explaining 74% of the variation in yield between years. Production of forbs also continued to be significantly correlated with mean temperature for May and precipitation from July-April, although the predictive capability of the resulting regression was diminished (R^2 = 0.720, F = 10.28, P = 0.007) compared to that derived from data for 1976-1982.

An examination of the residuals of this regression indicated that production during 1984 and 1986 deviated most. A regression of mean temperature for May and precipitation during July-April on forb production for the 9 years that excluded 1984 and 1986 had very high predictive power (R^2 = 0.941, F = 47.62, P = 0.0006). Data from the residuals of the full regression indicated it overestimated forb production when precipitation increased in years following drought. This apparently occurred because the regression could not account for moisture necessary to recharge soil moisture above the wilting point, when additional moisture becomes effective for plant growth.

As noted earlier, soil moisture measurements probably would be best correlated with forb yield because they encompass temperature, precipitation, and past conditions. In the absence of soil moisture measurements, the regression of mean temperature for May and precipitation during July-April gave adequate predictive power, providing it was recognized that yield was overestimated in the year of recovery following drought. Despite those overestimates, the regression accurately predicted trend in production (stable, increase, or decrease) in production from previous years.

Based on these findings, an index of relative summer forage production (Fig. 3.9) was computed for each year from 1959 through 1987 as forage yield estimates using the regression equation: [$\hat{Y}$ (forb and shrub yield) = 1,704 - 30.04 X_1 (mean temperature for May) + 24.61 X_2 (precipitation

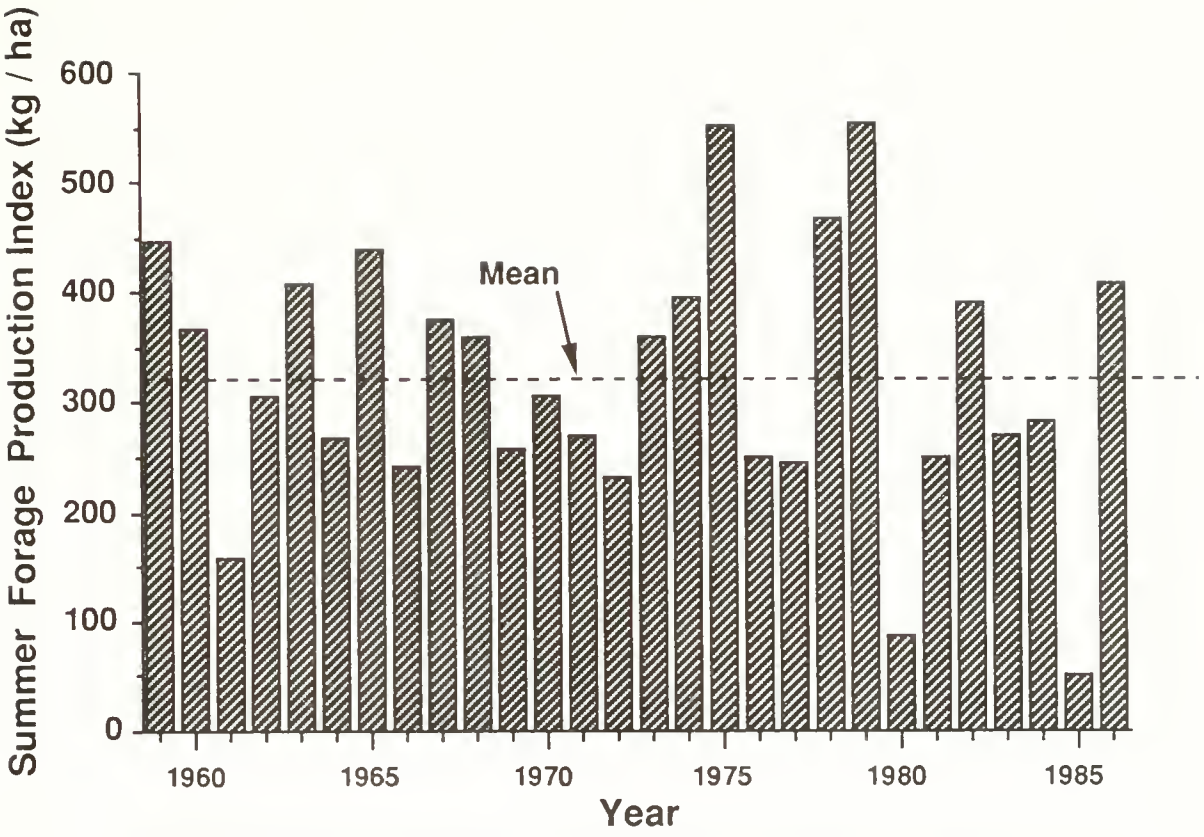


Figure 3.9. An index of summer forage production (kg/ha) for forbs and shrubs at selected sites on the Missouri River Breaks study area as determined by clipping and regression analysis.

July-April)]. This index indicated that 1961, 1980, and 1985 were years of extremely poor forage production on the study area, while 1959, 1965, 1975, 1978, and 1979 were characterized by forage production more than 1 standard deviation above the mean. Although production in other years, such as 1963, 1967, 1968, 1973, 1974, 1982, and 1986, was indicated to be less than 1 standard deviation above the mean, all stand out in field notes, general observations, or other data as years of above-average forage production.

Forage Abundance

Forage production was directly measured on only 4 sites in 2 vegetation types (Table 3.4), but a variety of data (e.g., Tables 3.2 and 3.3) were available to estimate the

relative abundance of the same species in other types. Those data were used to calculate estimates of total forage produced on the study area during summer and autumn. The estimates were developed with very conservative parameters that included the following:

1) Distribution cells in which deer were not observed during aerial surveys (17% of area) were not included in forage calculations although they undoubtedly received at least minor use by deer.

2) Minor vegetation-cover types in which relative forage abundance was not measured (an additional 9% of area) were either assigned no value for forage, or a level equivalent to the value in the lowest type measured. Several of these types (river riparian, pine-juniper-Douglas fir, and grassy bottoms) were probably above average in forage production.

3) Only those forbs known to be preferred by deer during summer and autumn were used to calculate forb production.

4) The production of 2 very important shrubs (rubber rabbitbrush and green rabbitbrush) was not estimated or included, although they often averaged up to one-third of the autumn diet.

5) Only one-half of the forage in the big sagebrush habitat in which deer were observed was considered usable.

6) After the previous 5 factors had been included in calculations, only one-half of the estimated forage yield was considered usable by deer.

7) Regrowth of forage plants was not considered.

An example of the data and calculations involved in these estimates is presented in Appendix B. The results (Table 3.8), together with data presented in Figure 3.9 indicated that the quantity of forage during summer and autumn was adequate to support existing deer populations throughout the period 1959-1986. Only in 1985, did the available quantity of forage during summer and autumn appear to approach a shortage. However, even then, given the conservative assumptions of the calculations and the fact that an autumn "green-up" of grasses and forbs occurred in 1985, it is unlikely that the quantity of forage was insufficient. Similar conclusions about the quantity of summer-autumn forage were made for a Colorado mule deer range (Wallmo et al. 1977).

Table 3.8. Estimated forage production on the study area and estimated number of deer it would support during summer and autumn, 1976-1986.

Year	Total kg of Forbs on Study Area	Total kg Forbs Available	Number of Deer Supported Summer-Autumn[a]
1976	1,375,136	464,213	1,719
1977	1,137,342	353,075	1,308
1978	7,375,912	3,009,784	11,147
1979	10,609,783	4,543,311	16,827
1980	1,037,409	327,102	1,211
1981	2,016,061	705,630	2,613
1982	3,226,553	1,214,169	4,497
1983	1,351,978	565,691	2,095
1984	616,985	227,705	843
1985	248,510	84,569	313
1986	3,900,078	2,232,415	8,268

Year	Total kg Summer-Autumn Shrub Species	Total kg Shrubs Available	Number of Deer Supported	Number of Deer Supported by Forbs & Shrubs
1976	1,282,604	641,302	2,375	4,094
1977	486,148	243,074	900	2,208
1978	2,450,196	1,225,098	4,537	15,684
1979	2,151,563	1,075,781	3,984	20,808
1980	489,131	244,565	906	2,117
1981	988,475	494,237	1,830	4,444
1982	1,081,635	540,817	2,003	6,500
1983	347,645	173,822	644	2,739
1984	742,405	371,202	1,375	2,218
1985	242,030	121,015	448	761
1986	2,018,451	1,009,225	3,738	12,006

[a] Number of deer supported = Estimated total kg forbs and/or shrubs available on study area / 1.8 kg per deer day / 150 days, summer-autumn period.

The quantity of forage available on the study area during winter and spring was not directly measured, however some observations indicated that it was unnecessary. Forage quantity or quality probably was not limiting during spring (April-June) because more green forbs were available then than during July when plots were clipped (Table 3.3). Also, deer made considerable use of ubiquitous new green grasses during spring.

The primary forage species used during winter (big sagebrush and Rocky Mountain juniper) were essentially unlimited in abundance. No hedging, highlining, or other indications of overuse of those species was noted. As pointed out by Wallmo et al. (1977), the total use of those species may be limited because of the bacteriocidal effects of their essential oils. Substantial use must be made of other species to dilute big sagebrush and Rocky Mountain juniper. Although most other forage available during winter, with the possible exception of rabbitbrush, were nutritionally below maintenance requirements for deer, adequate quantities were available to mix with big sagebrush and Rocky Mountain juniper.

Rabbitbrush was essentially used entirely every year, even at the lowest observed deer densities. At low deer densities, however, it may be available for a longer portion of the winter period, raising the average nutritional plane of deer.

Regardless of deer density, forage quantity appeared to be adequate, but forage quality, by itself, was probably inadequate, to sustain deer during any winter. Although winter forage supplied a portion of maintenance requirements, winter survival appeared to depend on fat accumulation and storage during summer and autumn, the length and severity of winter, and energy conservation behavior (Wood et al. 1962, Loveless 1967, Silver et al. 1969, Thompson et al. 1973, Bucsis 1974, Short et al. 1974, Mackie et al. 1976, Mautz et al. 1976, Walmo et al. 1977, Mautz 1978, and Youmans 1979).

Changes in Abundance and Use of Forage Plants

The percentage of current annual growth twigs or "leaders" on shrubs used by mule deer was recorded each year, beginning in 1959 for rubber rabbitbrush and 1960 for fragrant sumac (Fig. 3.10). These 25 plant transects were established according to the criteria of Cole (1958 and 1959) and originally included information collected on age, condition, and form class of the plants, as well as percent leader use. Transects were measured in spring of each year and, thus, recorded use for the previous summer, autumn, and winter. Although Mackie (1975) determined that these transects did not

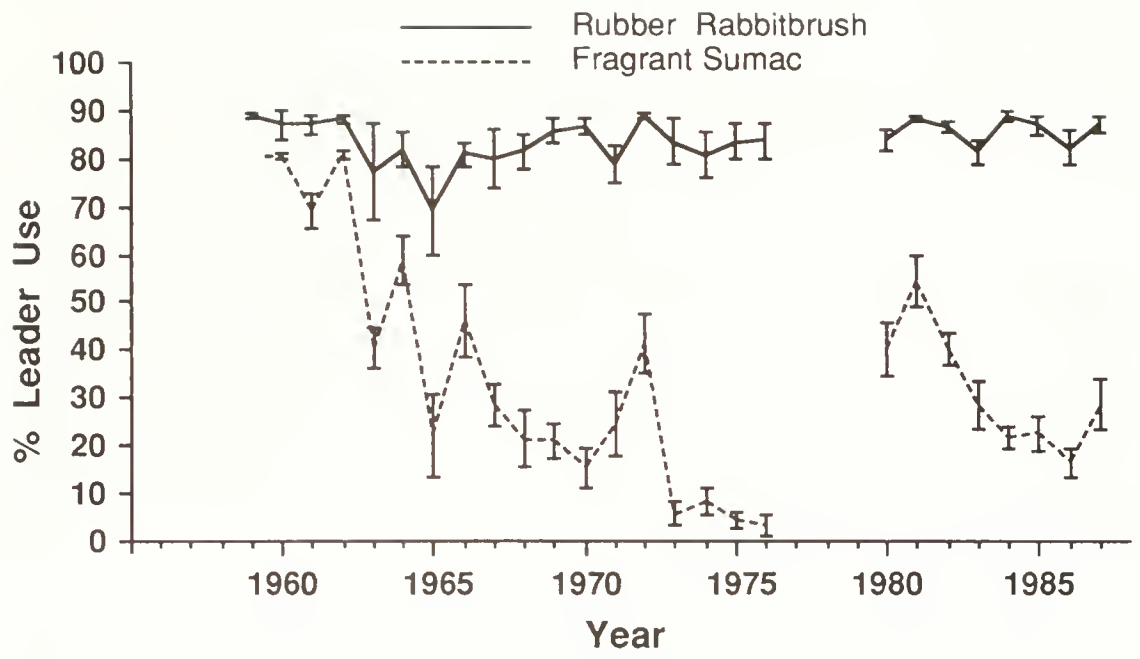


Figure 3.10. Trend in percent leaders used by spring each year for two important browse species, 1959-1976 and 1980-1987. Bars represent standard eror of the mean.

reliably measure what they were originally intended to (especially condition), some useful information was obtained.

One criticism of the Cole transects was that too few were established for each deer population to determine whether changes in use were statistically significant. Transect density on our study area was at about the highest level in the state. From 3 to 7 ($\bar{X}$ = 5.3) rubber rabbitbrush transects and from 2 (1960 only) to 10 ($\bar{X}$ = 7.2) fragrant sumac transects were measured each year.

The relative number of transects was high for our study area, but few statistical differences were observed in percent leader use among years (Fig. 3.10). Because utilization was measured by categories, 90% leader use was the highest possible value. The upper confidence level of leader use was never below 88% for rubber rabbitbrush during any of the 25 years of measurement. The lower confidence level was 30% during 1965 and 49% during 1963, but was usually always above 60% leader use. Annual mean percent leader use for rubber rabbitbrush was consistently high ($\bar{X}$ = 83.6$\pm$1.9 SE, range 69-

89, CV=0.055) throughout the entire period 1959-1986 despite wide fluctuations in deer numbers.

Annual mean percentage of leader used on fragrant sumac varied considerably ($\bar{X}$ = 33.2±9.5 SE, range 3-81, CV=0.68). Lowest use was recorded during both low (1973-1976) and high (1968-1970 and 1984-1986) deer population levels (Fig. 3.10).

From transects established during 1959-1963, data on longevity of tagged plants were available for 6 transects on fragrant sumac and 2 transects on rubber rabbitbrush. Because these transects of 25 plants were established using nearest neighbor (of the same species) techniques, new plants establishing between the original tagged plants could be detected. Deaths of tagged plants were recorded as they occurred through the years. Existing records were summarized and, during measurements in spring 1985, particular attention was given to dead tagged plants and new plants that had established over the years.

A total of 4 of 150 fragrant sumac plants had died on the 6 transects since 1963 and 19 new plants had established, for a net increase of 15 plants. A total of 4 of 50 rubber rabbitbrush plants had died on 2 transects, and 29 new plants had established, for a net increase of 25 plants. Although a few of the new shrubs may have been overlooked when the transects were first established, the overall conclusion was that the number of fragrant sumac and rubber rabbitbrush plants on those transect areas increased after 1963. Because we had increasing difficulty in finding 25 plants to measure within one rubber rabbitbrush transect area without tagged plants, we believe the number of rabbitbrush plants declined through the years on that area.

Line-intercept transects were established within mature stands (100+ years) in the pine-juniper and Douglas fir-juniper vegetation types in 1963 and remeasured during 1983. Within the pine-juniper type (Table 3.9), both ponderosa pine and Rocky Mountain juniper increased in coverage over the 20 year period, further closing the overstory. Significant increases in canopy coverage occurred for rubber rabbitbrush and green rabbitbrush, but canopy coverage of current, gooseberry, and snowberry declined significantly. Within the Douglas fir-juniper type (Table 3.10), canopy coverage of both Douglas fir and Rocky Mountain juniper increased significantly, but canopy coverage of Ponderosa pine declined. Among understory species, only canopy coverage of fragrant sumac increased significantly. Canopy coverage of rose, snowberry, gooseberry, and currant decreased significantly.

Table 3.9. Proportion of line intercept transects in Pine-Juniper habitat types covered by various shrub species, 1963 and 1983.[a]

Shrub Species[b]	1963	1983	Change From 1963	Z value
Artr	0.0008	0.0010	0	0.91
Chna	0.0007	0.0022	+	7.12**[c]
Chvi	0.0000	0.0004	+	11.11**
Jusc	0.0866	0.1446	+	23.51**
Rhar	0.0098	0.0088	0	1.33
Ribes spp.	0.0015	0.0011	-	2.00*
Pipo	0.2620	0.3073	+	13.00**
Rosa spp.	0.0096	0.0107	0	1.39
Symp spp.	0.0155	0.0070	-	10.38**

[a] Fourteen 100-foot lines at 4 permanently marked transects.
[b] See plant species list, Appendix C.
[c] * Significantly different at $P < 0.05$.
** Significantly different at $P < 0.01$.

Table 3.10. Proportion of line intercept transects in Douglas fir habitat type covered by various shrub species, 1963 and 1983.[a]

Shrub Species[b]	1963	1983	Change From 1963	Z value
Jusc	0.3116	0.3567	+	6.62**[c]
Rhar	0.0029	0.0094	+	5.87**
Ribes spp.	0.0046	0.0019	-	3.18**
Pipo	0.1931	0.1810	-	2.13*
Rosa spp.	0.0458	0.0177	-	11.07**
Prvi	0.0304	0.0343	0	1.00
Psme	0.5607	0.6290	+	9.61**
Symp spp.	0.0561	0.0495	-	2.10*

[a] Two 100-foot lines at each of 2 permanently marked transects.

[b] See plant species list, Appendix C.

[c] * Significantly different at $P < 0.05$.
** Significantly different at $P < 0.01$.

Overall, these data indicated that, in unburned timbered habitats, the trend during the last 20 years has been toward increasing overhead canopy, with a decline in coverage by snowberry, currant, gooseberry, and probably rose. Shrub species showing an increase, or at least no significant decrease, included fragrant sumac, rubber rabbitbrush, and green rabbitbrush.

Eichorn and Watts (1984) reported that burning of mature stands in the Douglas fir-juniper type on this area increased canopy coverage of snowberry, rose, and chokecherry. They also noted a similar increase in shrubs on burned pine-juniper types, though the ultimate increase and canopy coverage was less than occurred on the Douglas fir-juniper type.

As part of a study of the ecology of fragrant sumac in Montana, Martin (1972) established 5 point-center-quarter transect plots on the study area, each of which included 20 tagged fragrant sumac plants. These plants and transects were first measured in 1971 and subsequently remeasured in 1982 and 1986 (Table 3.11). None of the 100 fragrant sumac plants, tagged in 1971, were dead in either 1982 or 1986. Plant diameter, area, volume, corrected plant area, and corrected plant volume were all significantly greater in 1982 and 1986 than in 1971. The percent crown dead remained the same in 1982 as 1971, but there was significantly less percent crown dead in 1986 than in 1971 or 1982. Height was significantly lower in 1986 than 1982. Despite considerable girdling by microtine rodents in winter 1978-79, all fragrant sumac plants present in 1971 continued to live, and in aggregate, increased in area and volume.

Although, as noted above, all 100 fragrant sumac plants tagged in 1971 were still alive in 1986, point-centered-quarter measurements for 1972 and 1982 (Table 3.12) indicated a relative decline in the number, density, and frequency of plants. That resulted because the point-centered-quarter data gives relative values, not absolute values. The 2 sets of data (Tables 3.11 and 3.12) indicated that, although numbers of fragrant sumac and rubber rabbitbrush plants probably were similar in 1972 and 1982, the numbers of other shrubs, especially snowberry, had increased. Four of 5 of these sites had been burned more than 25 years previously and, as predicted by Eichorn and Watts (1984), some overstory sensitive shrubs may have continued to increase following initial measurements in 1972.

Collectively, the measurements indicated that increasing or at least stable shrub populations occurred on most transects despite 1 to 2 "irruptions" of the mule deer population over the intervening years, consistently heavy use of rubber rabbitbrush plants by deer, and at least occasional

Table 3.11. Size and condition of 100 tagged fragrant sumac plants on 5 plots within the Missouri River Breaks study area, 1971, 1982 and 1986.

Year	D1 Diameter (m)	D2 Diameter[a] (m)	Height (m)	Percent Crown Dead	Plant Area (m^2)	Plant Volume (m^3)	Corrected[b] Plant Area (m^2)	Corrected[c] Plant Volume (m^3)
1971	2.08±0.06[d]	1.54±0.05	0.75±0.03	23.8±2.2	2.66±0.16	2.14±0.18	2.08±0.15	1.69±0.16
1982[e]	2.38±0.07	1.89±0.06	0.89±0.03	23.8±1.9	3.74±0.21	3.60±0.29	2.96±0.19	2.90±0.26
1986[f]	2.43±0.07	1.88±0.05	0.84±0.03	19.1±1.7	3.80±0.21	3.48±0.28	3.15±0.19	2.95±0.26

[a] Diameter measured perpendicular to D1.

[b] Takes Percent Crown Dead into account.

[c] Takes Percent Crown Dead into account.

[d] Mean ± SE.

[e] All values for 1982 except Percent Crown Dead are significantly ($P \leq 0.05$) larger than 1971.

[f] All values for 1986 except Percent Crown Dead are significantly ($P \leq 0.05$) larger than 1971. Percent Crown Dead is significantly less ($P \leq 0.05$) than 1971. Height and Percent Crown Dead are significantly ($P \leq 0.05$) less in 1986 than 1982. No significant difference between other values in 1982 and 1986.

Table 3.12. Relative density, dominance, frequency, and number of various shrubs on 5 point-centered-quarter transects within the Missouri River Breaks study area, 1972 and 1982.

Species[a]	Year	Relative Density	Relative Dominance	Relative Frequency	Importance Value	Number of Plants
Rhar	1972	21.7	40.9	47.6	110.2	91
	1982	10.2	20.0	30.5	60.7	43
Syoc	1972	13.8	3.5	25.7	43.0	58
	1982	31.2	1.1	50.5	82.8	131
Ronu	1972	9.5	3.8	23.8	37.1	40
	1982	11.0	0.6	24.7	36.3	46
Chna	1972	7.6	4.7	18.1	30.4	27
	1982	3.6	0.3	9.5	13.4	15
Jusc	1972	12.9	34.1	27.6	74.6	54
	1982	11.7	52.3	24.8	88.8	49
Artr	1972	19.7	6.8	33.3	59.8	83
	1982	22.2	10.7	36.2	69.1	91

[a] See plant species list, Appendix C.

heavy use of fragrant sumac plants. Significant declines in shrub coverage was noted only in mature forested types where overstory coverage had increased. The decline in shrub coverage in these types probably resulted from successional trends rather than overuse by deer or other animals.

The considerable annual fluctuation in forage production was attributable to annual climatic variation and did not appear to be influenced by deer populations. Long term trends in forage abundance, in addition to being influenced by climate, appeared to be primarily affected by forest maturation and periodic wild fires.

Land Use

Prehistorically, the "breaks" apparently were a common hunting area for several Indian tribes; none maintained exclusive use of the area, especially over long periods of time. Overall human use of and impact on the land and wildlife was probably relatively low and intermittent. The journals of Lewis and Clark indicate an abundance of wildlife, including the newly described mule deer, in the vicinity of the study area in 1805. Major influent species, which occurred at that time but not at present, include bison (*Bison bison*), Audubon bighorn sheep (*Ovis canadensis auduboni*), grizzly bear (*Ursus arctos*), and wolf (*Canis lupus*).

Minor numbers of trappers and traders traversed the area from the early 1800s to the 1860s, when the use of steamboats on the Missouri River led to the first major influx of people. "Woodhawks" became established along the river to supply steamboats with wood, and a small "town" existed at a steamboat landing at Rocky Point on the north-central edge of the study area from the 1860s to the turn of the century. Rocky Point served as a rendezvous for a wide variety of people inhabiting the surrounding area. A short-lived attempt to establish a settlement (Carroll) in the northeastern corner of the study area occurred during 1874-1877.

Domestic livestock grazing, which persists as the major land use, became widespread during the early 1880s when large livestock companies moved cattle, sheep, and horses onto the study area and adjacent breaks and plains. The loss of at least half of all livestock in the area during the severe 1886-87 winter reduced total livestock numbers through the 1890s. At the same time, large livestock companies were replaced by an increased number of individual ranchers grazing smaller herds.

The Homestead Acts of 1905 and 1909 led to settlement and attempts to cultivate upland sites over much of the area. Settlement peaked during 1908-1914 and included development of

a school, post office, and store (Little Crooked) on the south-central edge of the study area and a post office (Wilder) in the north-central portion. It is notable perhaps, that the influx of humans and early agricultural efforts coincided with the longest continuous period of above-normal moisture (1907-1918) in the area since about 1850 (Fig. 3.11). Years of low and high moisture were interspersed during 1919-1929, resulting in abandonment of the most marginal homestead sites. Extreme drought during 1930-1940 and other factors led to abandonment of most remaining homesteads and general depopulation of the area. By 1960, there were only 3 headquarter ranches and 2 seasonal (haying and winter livestock feeding) operations located on the study area; there were none by the 1970s. The only current inhabitants are employees of the Charles M. Russell National Wildlife Refuge (CMRNWR), Sand Creek Field Station, developed along Highway 191 in the northwest corner of the area during the early 1980s.

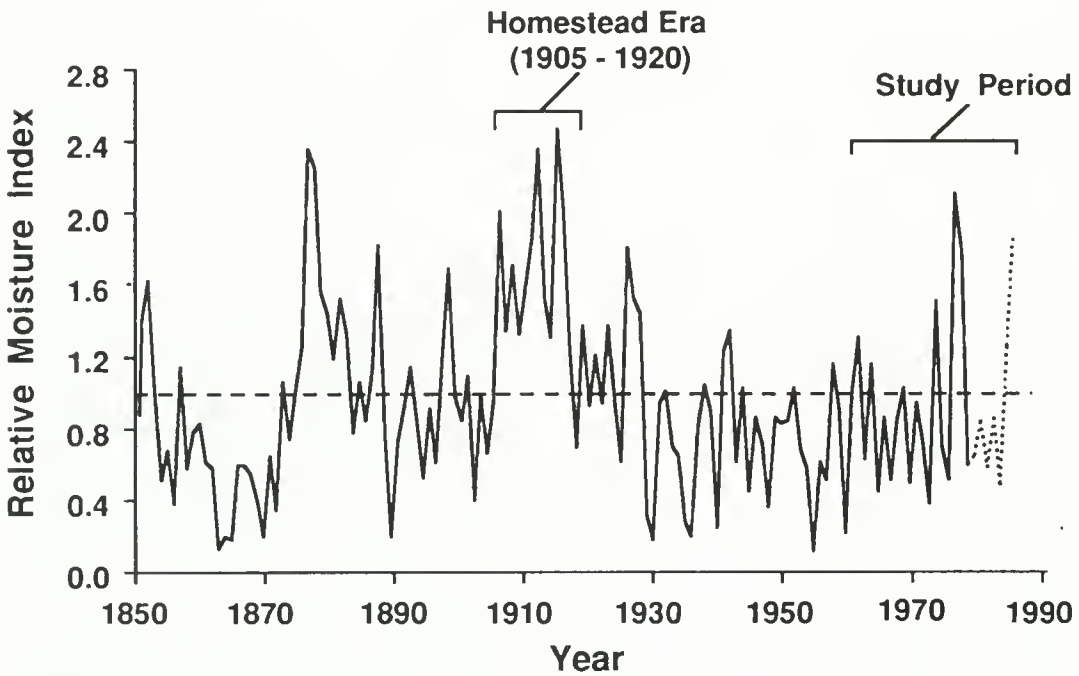


Figure 3.11. Relative moisture index for the study area during years 1850 through 1986 calculated from Douglas fir growth ring data. Estimates for 1981-1986 based on our regressions. See Fig. 3.8 for source acknowledgement.

Abandonment of homesteads resulted in reversion of nearly all formerly cultivated tracts to grassland and other native vegetation along with seeding of some fields to introduced crested wheatgrass (*Agropyron desertorum*). Alfalfa (*Medicago*

sativa) and barley (*Hordeum* spp.) were grown for hay and wildlife food on several river bottoms until the 1970s when all cropping of bottomlands was phased out and fields were allowed to revert to natural vegetation. The only remaining cultivation occurred as a small area of dryland grains on private lands on the extreme western edge of the study area.

Numerous tracts of land privatized during homesteading were repurchased by the Federal government following abandonment or to secure lands adjacent to the Missouri River for construction of the Fort Peck Dam which was completed in 1939. Publicly owned lands now comprise about 70% of the study area. About 45% lies within the CMRNWR, established in 1936 and administered by the U.S. Fish and Wildlife Service. Refuge lands are open to hunting of most Montana game species as provided for by State regulations for hunting districts which encompass the area. Except for about 5% owned by the State of Montana, remaining public lands are administered by the Bureau of Land Management.

For grazing purposes, most of the area has been administered as part of the East Indian Buttes State Grazing District, a large common allotment that also includes rolling plains to the southwest. The remainder consists of small units or pastures along the river bottom and two privately-owned upland tracts on which livestock were wintered until the 1970s. About 1600 animal units (AUs) are authorized; however, actual use on the study area has varied greatly from year to year and through time. Grazing is primarily by cattle, but a few horses were included through the years. Domestic sheep were grazed on adjacent plains and into the breaks along the southern edge of the study area until the 1960s.

Mule deer are the most common and abundant large wildlife species on the area. Others, in approximate order of abundance are Rocky Mountain elk (*Cervus elaphus*), white-tailed deer (*O. virginianus*), pronghorn antelope (*Antilocapra americana*), and coyote (*Canis latrans*). Mule deer, elk, and coyotes range throughout the study area, while whitetails are restricted largely to Missouri River bottoms and antelope range into the area along major ridges.

Elk, bison, and grizzly bear were essentially extirpated from the study area by the mid 1880s; wolves were gone by the 1920s. The present elk population developed as a result of release of 31 animals, transplanted from Yellowstone National Park, on the study area in 1951. Since then, numbers and distribution have increased consistently. Coyotes have always been present, but numbers apparently were low during the late 1940s and early 1950s when the toxicants strychnine and compound 1080 were first used in massive predator control

campaigns. Numbers gradually increased after the mid-1950s despite some continued control efforts with toxicants through 1971.

History of the Mule Deer Population

Mule deer apparently were common in the vicinity of our study area during the early 19th Century. As the Lewis and Clark expedition moved through the area in 1805, their journals note that on May 19 the party killed a minimum of 10 deer, on May 20, Clark killed two deer and "the hunters killed ... several deer merely for their skins", and on May 23, Clark killed four deer in the morning and saw a number of deer in the afternoon" (DeVoto 1953, Burroughs 1961). Later records suggest that deer also were common during the mid-to-late 1800s. Koch (1941), citing journals of his father and others wintering along the Missouri River immediately below our study area in 1869-70, states "[they] ...were able to go out every two or three days, about as one goes to the market now, and bring in a deer or antelope..." Similarly, Hornaday (1908) recounted a successful hunting trip for mule deer bucks in "bad-lands" along the Missouri east of our study area during October 1901. Up to that time deer apparently were so common that "...certain ranchmen of the North Side [of the river] had slaughtered great numbers of...deer to feed their dogs."

These sketchy early records indicate only that mule deer were widely distributed and occurred in some abundance during recent historical times. They tell us little about absolute or relative numbers or fluctuations through time. Of this we can only speculate based on more recent population characteristics and habitat relationships of mule deer in the area. It is unlikely, however, that deer were more widely distributed or generally more abundant in historical times than today. They may also have been subject to equal or greater temporal fluctuations in occurrence.

Relative moisture indexes calculated from tree-ring data (Fig. 3.8) indicate consistently wide variation in environmental conditions through the years. Periods of drought were interspersed with years of ample moisture, and mild with severe winters. Relatively dry to average conditions prevailed during the time of the Lewis and Clark passage through the area and during the 1860s and 1870s. The 1880s were relatively moist and included the exceptionally severe winter of 1886-87 during which more than half of the cattle herds in the area died. Deer must have suffered substantially as well. All of this would suggest that mule deer numbers and distribution probably fluctuated greatly throughout the 1800s and earlier as they do today.

Recollections of long-time residents of the area indicate that deer numbers were relatively high during 1890s and early 1900s but declined to scarcity during the 1920s and early 1930s. This decline, which coincided with great increase in human populations on the area during 1905-1920 and drought from the mid 1920s through the mid 1930s, was also documented in increasingly restricted hunting regulations. A 4-month hunting season with a bag limit of 8 deer established in 1895 was progressively reduced to 3 months and 3 deer in 1905, 2 months and 3 deer (of which 2 had to be bucks) in 1913, 2 months and 1 deer of either sex in 1919, and 2 months and "one male deer with visible horns" in 1921. From 1921 to 1930, the eastern sixty percent of the study area was closed to hunting and, during 1931 and 1932, the entire area was closed. Hunting resumed for bucks-only in 1933, but was prohibited on the portion of the area within the CMRNWR from 1937 through 1947 and during 1949.

An August 1935 survey of the area that later became the CMRNWR by O.J. Murie indicated that "the mule deer has become very scarce on some parts of this range, but is still present and widely distributed."

The period from the 1920s to 1935-1937 marked the historical low in mule deer populations on the study area. Some deer persisted, however, and by the time the drought ended in 1938, most of the human population had left the area, formerly cultivated tracts had reverted to rangelands, and the overall intensity of human usage had been greatly reduced. All of this apparently set the stage for increasing mule deer numbers during the late 1930s into the 1940s (Mackie 1970).

The newly established Fort Peck Game Range brought resident observers with biological interest to the area during the late 1930s. Quarterly narratives by Game Range personnel, beginning in 1940, provided qualitative information on wildlife abundance and forage and cover conditions through the 1940s and 1950s. Passage of the Pittman-Robertson Act and its adoption by the Montana Legislature in 1941 enabled the Montana Fish and Game Department to employ biologists and begin collecting quantitative data on and near the study area during 1947.

Selected statements from quarterly narratives and other reports during 1940-59 that relate to mule deer populations and factors that we have found to influence mule deer populations are presented in Appendix D. The reader is encouraged to read Appendix D to obtain more specific information as well as "the flavor of the times". Although such qualitative information does not enable us to precisely estimate numbers, it was recorded every year and provided a continuous record of impressions and events. When combined

with the more scattered and diverse quantitative data available (e.g. early censuses), and both are interpreted in light of findings from our studies during 1960-87, we believe that reasonable estimates of mule deer numbers and trends during the period can be derived.

Deer were still considered scarce in 1940, but immediately thereafter and through 1947, the narratives (Appendix D) indicated that mule deer populations increased rapidly. Concurrently, range and forage conditions were considered "excellent" through 1947. A deer drive count on 4 mi^2 in autumn 1944 produced an observed density of 8.5 mule deer/mi^2. More recent information from that same area indicates that the actual density could have been as high as 11-17 mule deer/mi^2. In 1948, deer were considered sufficiently abundant to permit hunting of bucks within the Game Range for the first time since it's establishment in 1935. Also, Game Range managers and state personnel were starting to discuss the "unmentionable proposition of opening the season on does."

The first substantial quantitative data on mule deer populations were collected by aerial strip census during September 1947 (Brown 1947, Appendix D, Table 3.13). Aerial strip censuses were also conducted during February 1948, 1950, and 1951. These censuses recorded observed densities ranging from 3.4 to 5.7 mule deer/mi^2. Our adjustments of those figures (Appendix D, Table 3.13), based on the areas flown and our more recent comparative information, indicate actual densities of 7-12.5 mule deer/mi^2. The lowest estimated density (5-8/mi^2) was observed during mid-late winter 1950, the second of 2 consecutive severe winters. Pre-hunting season density may have been as high as 15-18 mule deer/mi^2 in autumn 1951 (Appendix D).

Good forage conditions prevailed from 1951-1954, but drought and poor forage conditions occurred from mid-summer 1955 through 1958. Fawn survival was good during the early period, but had declined by 1958-59.

An attempt to remove all deer from a 3.13 mi^2 fenced pasture adjacent to our study area in February 1958 indicated a minimum density of 7.7 mule deer/mi^2 (Appendix D, Table 3.13).

The accuracy of early population estimates is subject to question, especially when the individuals reporting and interpreting them did not do the work. We believe, however, that the estimates, and especially the ranges presented (Table 3.13, Appendix D), are reasonable.

Table 3.13. Density estimates for mule deer in northeast Fergus County, Montana, 1944-1958.

Date	Type of Census	Density Estimate (Range)	Remarks
1943	Unknown -- probably minimal ground counts of selected areas or "a guess."	1.3/mi^2 0.5/km^2	Probably substantial underestimate.
20 Oct. 1944	Drive count of 4 mi^2 by 2 people walking.	8.5/mi^2 3.3/km^2	Small area sampled.
Sept. 1947	Aerial strip census.	12.6/mi^2 4.9/km^2 (10-15/mi^2)	Reasonable. ±20%
Feb. 1948	Aerial strip census.	8.0/mi^2 3.1/km^2 (6-10/mi^2)	Reasonable. ±20%
Feb. 1950	Aerial strip census.	6.7/mi^2 2.6/km^2 (5-8/mi^2)	Probably low. ±20%
Feb. 1951	Aerial strip census.	10.0/mi^2 3.9/km^2 (8-12/mi^2)	Reasonable. ±20%
Feb. 1958	Attempted total kill within 3.13 mi^2 pasture.	7.7/mi^2 2.95/km^2	Reasonable, small area sampled.

Collectively, information and data on historical deer numbers and trend indicate mule deer were at least moderately abundant in the vicinity of our study area throughout the 1800s and early 1900s. Thereafter, mule deer populations on our area declined to historic low levels by the early 1930s, but started to increase by the late 1930s and especially early 1940s. The increase in deer numbers after the 1930s has been attributed by various people to the following factors, both singly and in combination: 1) human depopulation of the area - both as a harvest effect and a habitat recovery effect; 2) increased precipitation - the ending of the drought; 3) predator control; and 4) increasingly effective law enforcement.

Most of the historically highest human population on the area during the teens and 1920s had abandoned their homesteads

and left the area by 1940. These people had to a large extent depended on deer for subsistence and hunted yearlong. The onset of World War II further reduced the population of young men living near the area and war-time rationing of ammunition, tires, and gas further reduced hunting pressure by people from the surrounding area. As Holibaugh (1944) stated, "Perhaps the tire and gas situation has eliminated to a certain extent the hunting, both illegally and legally."

Many factors, including illegal hunting; habitat disruption by homesteading, plowing, and timber harvest; severe drought; and vegetation depletion by domestic livestock grazing and grasshoppers (Murie 1935) probably contributed to the decline in deer numbers. The increase in mule deer probably resulted from a decrease in the influence of the above factors, and especially from improved forage conditions. The increase in mule deer numbers coincided with the improved forage conditions that resulted from increased precipitation during 1938, 1941-44, and 1946.

Predator control is the most often cited reason for the increase in deer and antelope during the 1940s, both locally and throughout the western United States. Information from this area indicated that mule deer on this area had reached historically high levels by autumn 1947 and possibly as early as 1944. However, the narratives indicate that no substantial, effective coyote control program began until December 1946. Sporadic trapping and very limited poisoning in local areas took place prior to that. Indeed, the narratives and coyote damage complaints indicate that coyote populations and depredation increased from 1940-1946! Mule deer populations had apparently reached such high levels prior to 1947 that Federal biologists already considered the deer range to be approaching "overuse".

The evidence did indicate that intensive predator control during the late 1940s and early 1950s resulted in increased mule deer fawn survival, at least through 1956. This increase in fawn survival, however, apparently did not result in much, if any, increase in mule deer populations within the riverbreaks habitat. Our recent information on mule deer dispersal does substantiate, however, local suspicion that predator control may have helped create an "excess" that successfully recolonized surrounding areas of less secure habitat. Although mule deer population recovery occurred within the riverbreaks habitat prior to effective predator control, it may have occurred even faster had predator control been implemented earlier.

Yearlong subsistence hunting undoubtedly contributed to low deer populations in the 1920s and 1930s. It is unlikely that the restrictions on hunting effectively protected deer to

any great extent. Enforcement was largely lacking, and during the homestead era as well as through subsequent periods of drought and depression, residents shot deer as need and opportunity presented. Depopulation of the area, rather than increased law enforcement, probably contributed most to the decline in illegal harvest of deer.

Mule deer populations increased throughout the improved range conditions of the 1940s and declined somewhat during the severe winters of 1948-49 and 1949-50. Populations may then have increased during good conditions in the early 1950s, but declined following drought during 1955 and 1956.

Regardless of population level, and in spite of consistently "overused" browse species after 1948, deer apparently remained "in excellent condition", "very fat", and "one of healthiest and most productive [herds] in the country". This seemed to be uniformly true except during periods of drought (mid-late 1950s), when deer were in "bad condition", regardless of numbers. We believe the available data are sufficient to indicate that from 1947-1959, and possibly back to 1944, the mule deer population on our study area fluctuated within the same range of densities as it did during the period 1960-1987.

CHAPTER 4

POPULATION CHARACTERISTICS

Numbers and Density 1960-1987

Estimated total numbers of mule deer on the study area during autumn, early winter, and spring from 1960 through 1987 are shown in Figure 4.1. Annual and seasonal numerical population estimates by sex and age class are presented in Appendix A.

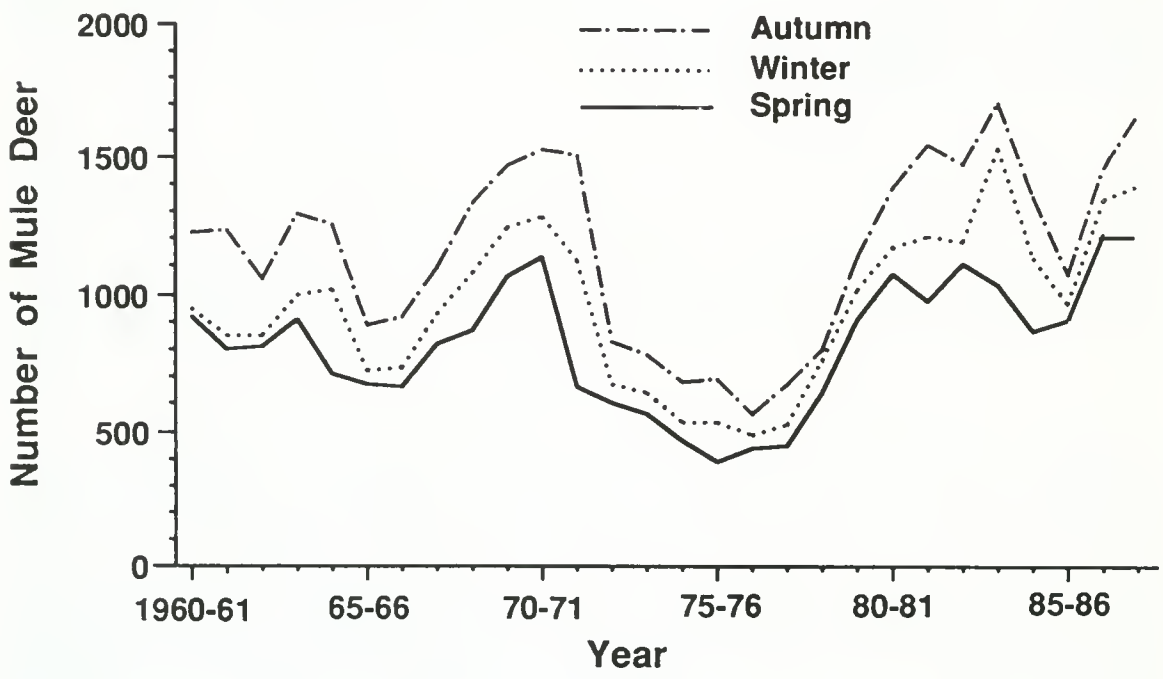


Figure 4.1. Estimated total number of deer on the study area during autumn, early winter, and spring, 1960-1988.

Approximately 1225 mule deer were on the area during autumn 1960 when, as a result of good recruitment of fawns, the population was probably at least somewhat higher than during 1959 (Fig. 4.1). Relatively minor fluctuations in population numbers occurred through autumn 1964. A major population decline occurred during the severe winter of 1964-65, reducing the 1020 deer entering winter to 715 deer (-30%) by spring 1965. The number of deer remained stable through spring 1967 and then started an increasing phase with the addition of the large 1967 cohort. That increasing phase lasted through spring 1971. High mortality during the severe winter of 1971-72 reduced the 1130 deer entering winter to 665 survivors (-41%) by spring 1972. From that point, a slow, gradual decline in deer numbers through 1976 occurred despite good weather and forage conditions during 1973-1975. Beginning with high survival of the 1978 fawn cohort, the mule deer population then increased through early winter 1983, reaching an autumn peak of 1715 deer and an early winter peak of 1545 deer. High mortality of fawns and relatively high mortality of adult females during winters 1983-84 and 1984-85 reduced total numbers of deer to 870 by spring 1985. Although initial production of fawns was poor during 1985, those alive during autumn survived well and a population increase started that has lasted through early winter 1987.

The total mule deer population varied by up to 3-fold within any season from low to high during 1960-1987 (Fig. 4.1). Maximum difference between the lowest spring (390 deer in 1976) and highest autumn population estimates (1715 deer in 1983) was 4.4-fold. Numbers of adult females fluctuated less than other sex/age groups, varying about 2.75-fold within seasons and 3.1-fold between lowest spring numbers and highest autumn numbers (Fig. 4.2). Numbers of adult males fluctuated from about 3.5 to 4-fold seasonally, and 6-fold from lowest spring to highest autumn population (Fig. 4.3). The number of fawns in the population varied about 5-fold in autumn and early winter populations and about 13.5-fold for recruited fawns in spring (Fig. 4.4). Highest number of fawns in autumn was about 17.5 times greater than the fewest recruited fawns in spring. Trends in fawn recruitment preceded trends in adult populations by one year (Figs. 4.2, 4.3, and 4.4).

During 1960-1987, the mule deer population varied in density from a low of 1.4/km^2 during spring 1976 to a high of 6.2/km^2 during autumn 1983. Because deer were not observed on 17% of the study area during any aerial surveys, ecological density was higher than absolute density. For generally occupied deer habitat, density was 1.7/km^2 during the population low and 7.5/km^2 during the high. Deer numbers and density were actually higher at birth pulse during mid-June (up to 9/km^2), but we did not consider fawns effectively added to the population until weaned, just prior to the hunting

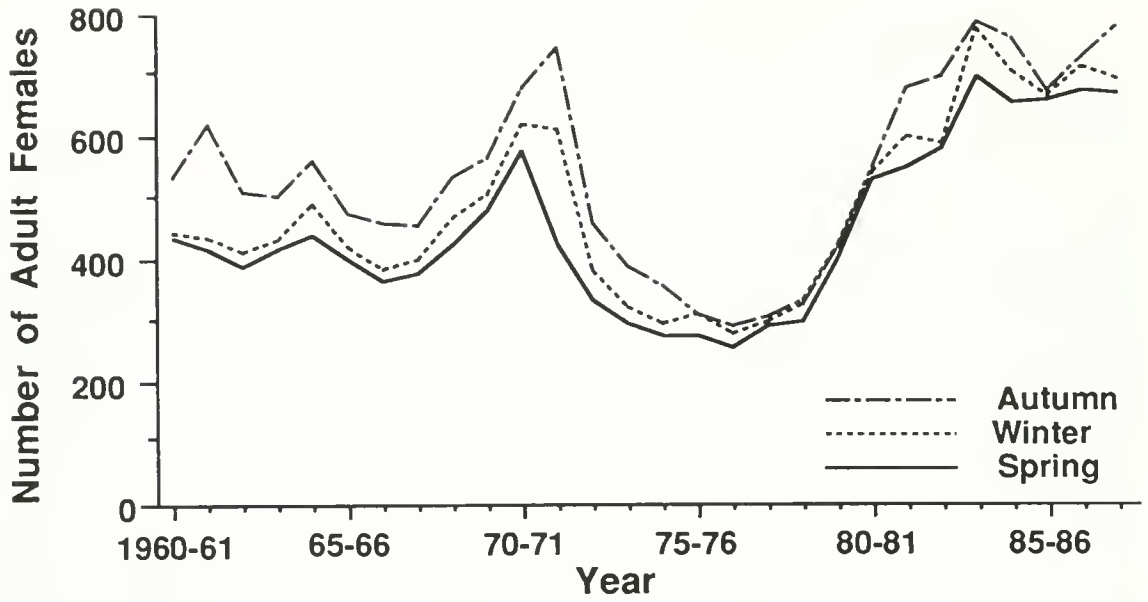


Figure 4.2. Estimated number of adult female mule deer on the study area during autumn, early winter, and spring, 1960-1988.

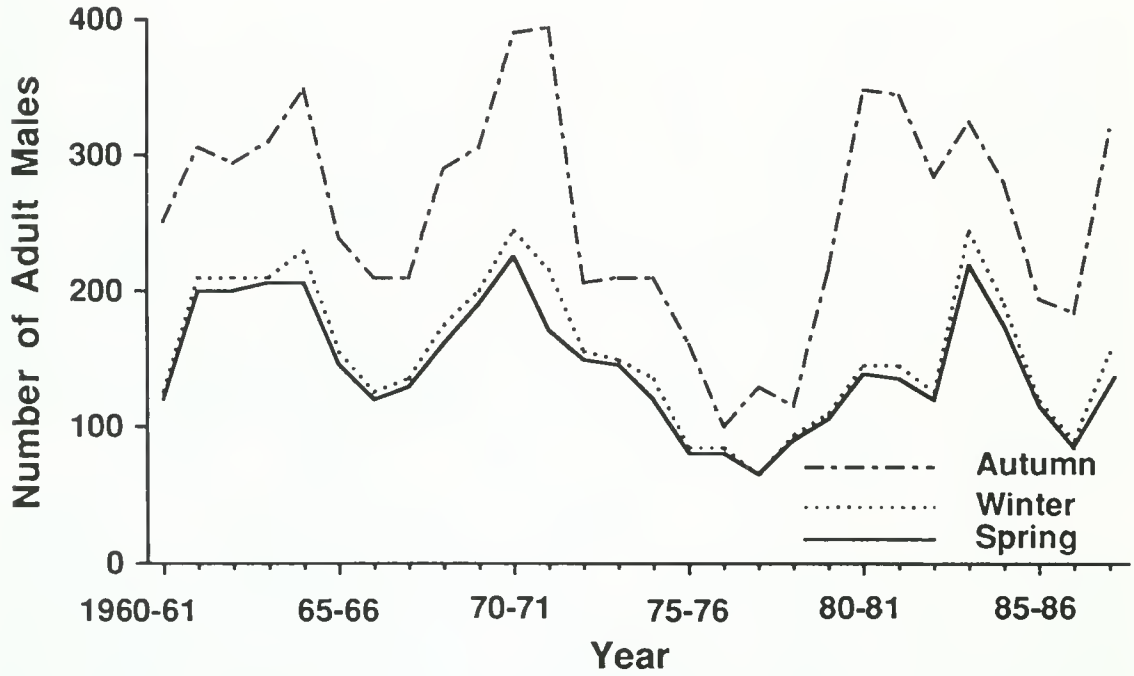


Figure 4.3. Estimated number of adult male mule deer on the study area during autumn, early winter, and spring, 1960-1988.

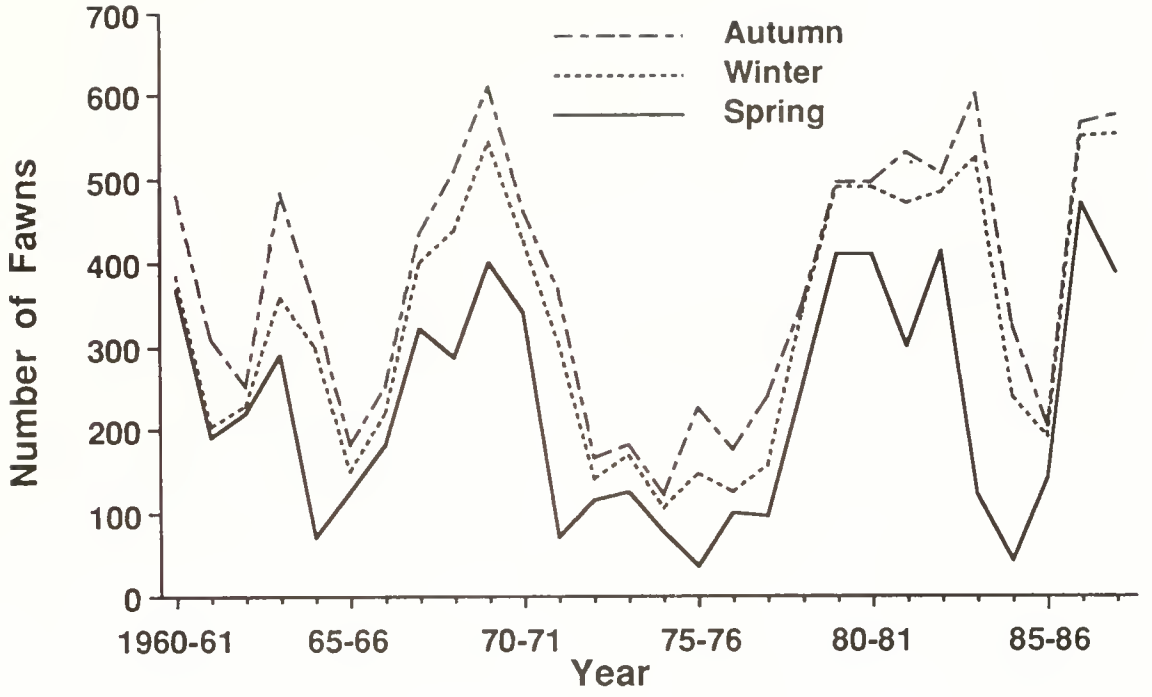


Figure 4.4. Estimated number of fawn mule deer on the study area during autumn, early winter, and spring, 1960-1988.

season. Density also varied across the study area. For example, a 21-km^2 area along the Missouri River on the northwestern portion of the study area had mule deer densities of 12-13/km^2 during autumn at population peaks.

Log plots (Ln) of population one year (N_t) against population the next year (N_{t+1}) for early winter (Fig. 4.5) and spring (Fig. 4.6) indicate the general cyclical nature of the population and/or time-lag effects. These data and those in Figures 4.1 through 4.4 also indicate, however, that time-lag effects, if they occurred, were not uniform and that population growth and decline occurred at a wide variety of overlapping population densities.

Population Growth Rates and Perspective 1930-1987

The maximum observed annual instantaneous rates of population growth ($r = LnN_{t+1} - LnN_t$) during the period 1960-1987 varied from r=0.30 to r=0.38 during winter-to-winter and spring-to-spring periods 1977-1980 and 1985-1987. Both periods of highest observed population growth rates occurred when harvest of antlerless deer was not legal. However, those growth rates did include harvest loss of adult males as well as natural mortality of all sex and age classes. If no adult males had been harvested during biological year 1979, but all

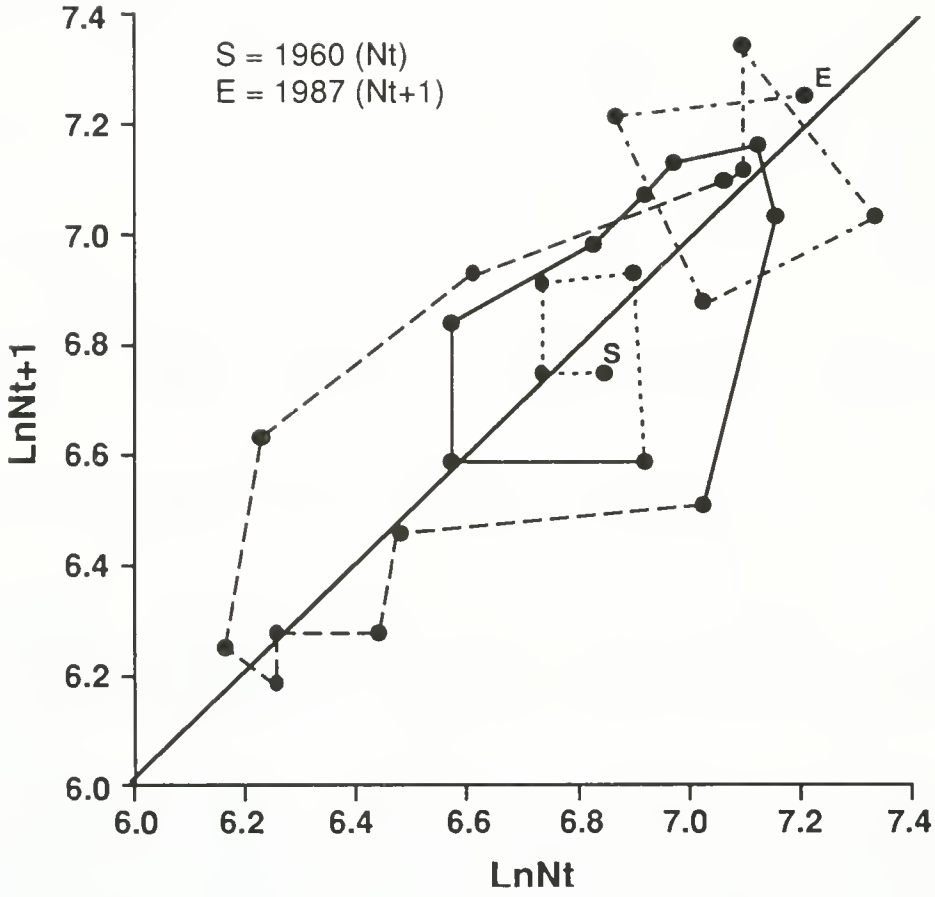


Figure 4.5. Plot of natural log Nt vs. natural log Nt+1 for the early winter mule deer population, 1960-1987, indicating rate and direction of change in population growth in relation to population level. Starting at S and following the points, lines moving above the horizontal indicate increased population (positive growth rate). Distance of the point above or below the 45 degree line indicates growth rate or decline. Type of line changes with each full population cycle (e.g., from low to high to low).

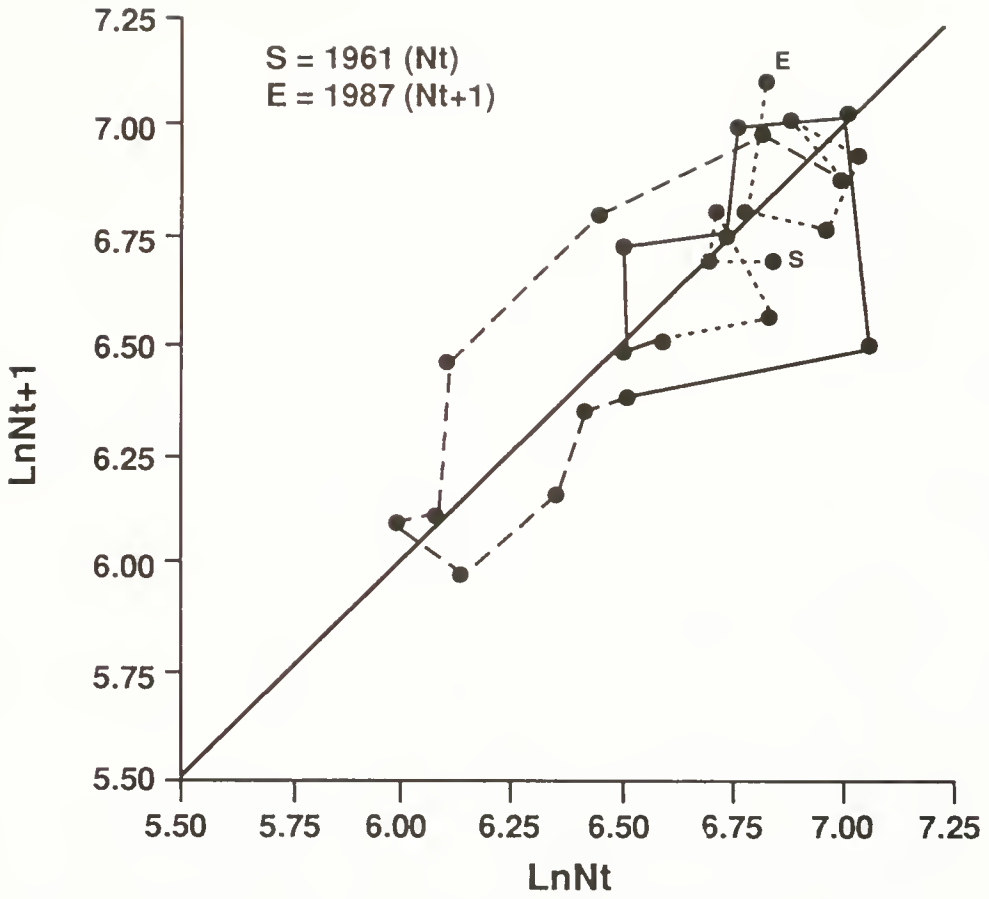


Figure 4.6. Plot of natural log Nt vs. natural log Nt+1 for the spring mule deer population, 1961-1987, indicating rate and direction of change in population growth in relation to population level. For description of how to interpret this figure, refer to Fig. 4.5.

other recruitment and mortality had remained the same, the population growth rate would have been r=0.466, approaching the 0.509-0.516 growth rates observed for white-tailed deer on The George Reserve over 6 and 7 year periods (McCullough 1983).

If all fawns born during 1979 were recruited and no mortality of adults had occurred, the instantaneous growth rate would have been r=0.602. However, because fawn production during 1979 was the highest ever recorded and natural mortality was very low, an instantaneous growth rate of 0.466 might be about the maximum realistically expected. The maximum potential growth rate could have been higher, however, during an initial year with a different female age structure than occurred during 1979.

Because mule deer on this area, and most others, seldom breed as fawns, potential growth rate of the population can be influenced by female age structure (proportion of yearlings in June population). Few yearlings occurred in the population during spring 1978 as compared to spring 1979. If fawn production in 1978 had been equivalent to that of 1979 and no adult or fawn mortality occurred, the instantaneous rate of growth for the population would have been r=0.758. The difference between maximum potential growth rates for 1978 (0.758) and 1979 (0.602) was a result of differing proportions of nonproductive yearlings in the population. Because of the increasing number of recruited fawns, a maximum potential growth rate of 0.758 cannot be sustained, even without mortality, unless substantial net emigration of yearlings occurs. The large proportions of non-reproducing yearlings reduce the maximum instantaneous growth rate to about r=0.500 (0.479-0.513) in subsequent years. These calculations indicated that the spring-to-spring population growth rate observed for 1979-80 (r=0.352) was near the maximum sustainable, given hunting mortality of males.

High instantaneous rates of growth were not sustained for long periods during 1960-1987. An observed r=0.350 was sustained for 2 years from spring 1978 through spring 1980. Extended through spring 1981, the average instantaneous growth rate was 0.292 and through the 5 years of population increase ending in spring 1983, r=0.182. Some natural mortality of all deer and hunting mortality of adult males occurred throughout the 5-year period. Also, net emigration of yearling females occurred during spring 1980 and 1981, a more severe winter than average occurred during 1981-82, and hunting mortality of females and fawns was added during the fourth and fifth years of population growth.

Average instantaneous growth rates of 0.159 occurred for a 3-year period and 0.135 for a 4-year period during 1967-

1971, concurrent with moderately heavy hunting harvests. It is also possible that some net emigration of yearlings occurred during those years.

To place population fluctuations and growth rates of 1960-1987 in perspective for later theoretical discussions, we need to include estimates of earlier population levels, back to about 1930 (Fig. 4.7). Although the population estimates indicated by the dashed lines in Figure 4.7 cannot be precisely verified, historical notes discussed earlier (Chapter 3) indicate their general validity.

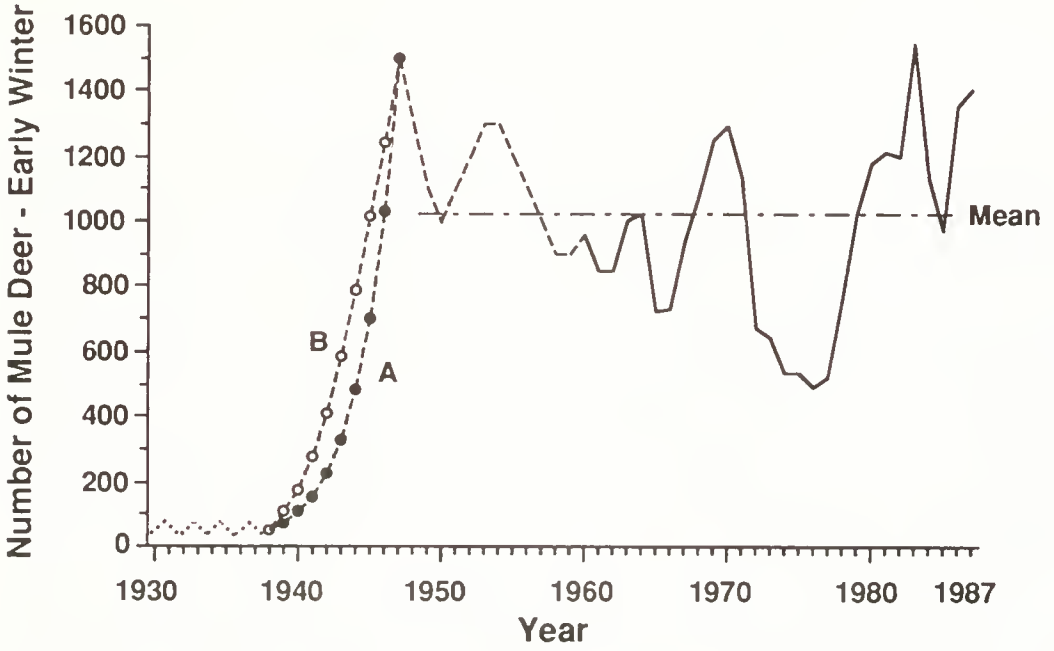


Figure 4.7. Estimated mule deer population levels during early winter, 1930-1987. See text for derivation of estimates prior to 1960 and for explanation of curves A (stable growth rate) and B (semi-logistic growth).

Mule deer populations during the early to mid 1930s were extremely low. Old timers talk about the rarity of seeing deer and that seeing a fresh deer track during this period was cause for excitement. When we compare these recollections to our observations during low deer numbers in the mid 1970s (400 deer, 1.5/km^2), we believe that fewer than 100 deer (0.4/km^2) probably occurred on the study area during the mid-1930s. For purposes of calculation, we chose 50 deer (0.2/km^2) as a reasonable estimate of the low.

We also know that population growth began during 1938 or 1939. Deer numbers increased progressively through 1947 or 1948, apparently reaching a population high that couldn't have been much higher than 1500 deer based on both a reasonable aerial strip census estimate plus 20% and practically achievable population growth rates. The population increase was probably halted by emigration of yearlings and mortality during the severe winters of 1948-49 and 1949-50.

Between 1938 and 1948, the population grew in a manner similar to that illustrated (Fig. 4.7), regardless of the degree of certainty about the number of years or deer involved. Depending on the number of years involved (8-10) and initial (25-100) and ultimate deer numbers (1200-1500), the average instantaneous rate of growth for the deer population was in a range of r=0.248-0.484.

Based on growth rates observed during 1960-1987, growth rates in the projected range were achievable during 1938-1948, although a sustained growth rate of 0.484 over 8 years was unlikely. There was at least some hunting loss of adult males during those years and at least a minimal amount of illegal kill of all deer and natural mortality of adult females and fawns must have occurred. Thus, we believe it is reasonable to assume that the average instantaneous growth rate during the period 1938-1947 was less than 0.484. The use of 50 deer in 1938 for a starting point and 1500 deer in 1947 as the population peak (Fig. 4.7) yields an average annual instantaneous growth rate of r = 0.378, near the midpoint of the potential range.

Growth curve A (Fig. 4.7) represents an annual growth rate of 0.378 between 1938 and 1947. It is unlikely that the growth rate was precisely the same each year, so the shape of the actual growth curve probably varied somewhat from that plotted. An alternative growth curve (B, Fig. 4.7) assumed a growth rate that decreased steadily with density (semi-logistic) as observed by McCullough (1983) for white-tailed deer on the George Reserve. That curve assumed a maximal growth rate of 0.76 for the initial year, a decline to 0.50 the second year, and then progressive declines with density to about 0.20 during 1946-47. Other alternative growth patterns exist, but none deviate significantly from the general pattern displayed in Figure 4.7.

During the period 1938-1948, the population probably grew in a manner similar to irruptive or introduced populations (McCullough 1979 and 1983, Caughley 1970). Subsequent to 1948, the population fluctuated widely around what some might call an "equilibrium density" of 3.8 deer/km^2. The major body of theoretical population work centers around the irruptive

growth phase of populations. Our results are mainly concerned with the fluctuations of an established population.

Population Composition

Sex Ratio

Three separate data sets, each collected over periods of 7-12 years, provided estimates of sex ratio among fawns from birth through 6-9 months of age. A ratio of 110 males:100 females was indicated by a combined sample of 218 newborn fawns captured and marked during mid-June. Ratios of 93 and 106 males:100 females were indicated by samples of 145 fawns killed by hunters and 74 fawns captured and marked during winter, respectively. Those ratios were not significantly different from each other or from a 1:1 ratio (chi square tests, all $P > 0.50$). The overall average (103 males:100 females, n=437) indicated that sex ratios were nearly equal or slightly favored males during the first year of life as generally reported in the literature. Sample sizes were inadequate to detect possible differences among years.

Among adults, females always outnumbered males (Tables 4.1 and 4.2). Classification in autumn, prior to the hunting season, averaged 42 males:100 females (range, 20-64:100). Early winter (post-season) ratios averaged 31 males:100 females and ranged from 13 to 50:100. The decline in proportion of males to females after the first year is not surprising in a population where males are harvested more heavily than females; though other factors may also have been involved. Martinka (1978) found adult females to outnumber adult males by more than 2:1 in an unhunted mule deer population. Gavin et al. (1984) reported 3 females per male and Kie and White (1985) 2.6 females per male in unhunted populations of white-tailed deer.

Sex ratios fluctuated widely among years as a result of variable and selective hunting pressure and variable fawn recruitment. Because of the relatively smaller numbers of adult males compared to females, the annual cohort of yearlings made up a larger portion of the male population than the female population. Population estimates indicated that yearlings comprised an average of 18% (3-30%) of the female population and 43% (10-66%) of the male population.

Age Structure

Fawns As A Proportion Of The Population

At birth pulse, newborn fawns comprised up to 55% of the population. Because fawns experienced higher mortality rates than adults, the proportion of fawns declined from June

Table 4.1. Mule deer population composition, determined from autumn ground and aerial surveys, 1960-86, Missouri River Breaks study area.

Year	Type of Observation	Number Classified	Percentage			Ratios		
			Adult Males	Adult Females	Fawns	Males:100 Females	Fawns:100 Females	Fawns:100 Adults
1960	Ground	347	18.5	42.9	38.6	43.0	89.9	62.9
1961	Ground	271	15.9	56.1	28.0	28.3	50.0	39.0
1962	Ground	92	28.3	50.0	21.7	56.5	43.5	26.3
1963	Ground[a]	142	28.9[a]	35.9[a]	35.2[a]	80.4[a]	98.0	54.3[a]
1975	Aerial	105	18.1	47.6	34.3	38.0	72.0	52.2
1976	Aerial	159	19.5	49.7	30.8	39.2	62.0	44.5
1977	Aerial	112	17.9	45.5	36.6	39.2	80.4	57.7
1978	Aerial	176	18.8	39.2	42.0	47.8	107.2	72.5
1979	Aerial	278	20.6	36.1	43.3	57.0	120.0	76.4
1980	Aerial	545	25.5	39.6	34.9	64.4	88.0	53.5
1981	Aerial	677	22.3	43.7	34.0	51.0	77.7	51.5
1982	Aerial	501	19.2	46.9	33.9	40.9	72.3	51.4
1983	Aerial	715	20.4	45.3	34.3	45.1	75.6	52.1
1984	Aerial	489	21.9	54.8	23.3	39.9	42.5	30.4
1985	Aerial	398	15.3	64.8	19.8	23.6	30.6	24.8
1986	Aerial	397	10.6	53.4	36.0	19.8	67.5	56.3
1960-86	Mean		19.5	47.7	32.8	42.2	73.6	50.1

[a] Percentage males and male:100 female ratio considered inaccurate and were excluded from the mean.

Table 4.2. Mule deer population composition during December or early January, as determined from ground and aerial surveys, 1960-1987, Missouri River Breaks study area.

Year	Type of Observation	Number Classified	Percentage			Ratios			% of Males that were Yearlings
			Males	Females	Fawns	Males: 100 FF	Fawns: 100 FF	Fawns: 100 AD	
1960-61	Grounda	668	9.3	48.6	42.1	19.1	86.4	72.6	56
1961-62	Ground	430	15.5	60.7	24.0	25.3	39.5	31.5	74
1962-63	Ground	190	19.5	52.1	28.4	37.5	54.5	39.7	63
1963-64	Aerial[b]	362	16.0	45.6	38.4	35.1	84.2	63.3	47
1964-65	Aerial	611	22.7	47.8	29.5	47.6	61.6	41.7	47
1965-66	Aerial	434	21.4	58.1	20.5	36.9	35.3	25.8	33
1966-67	Aerial	289	17.3	52.6	30.1	32.9	57.2	43.1	46
1967-68	Aerial[c]	115	20.0	40.0	40.0	50.0	100.0	66.7	
1968-69	NCRCA [d]	153	18.3	41.8	39.9	43.8	95.3	66.3	
1969-70	Aerial[e]	110			39.1			64.2	
1970-71	Aerial	776	18.8	48.1	33.1	39.1	68.9	49.5	47
1971-72	Aerial	679	19.0	53.8	27.2	26.1	50.6	37.4	46
1973-74	Aerial	370	24.1	49.5	26.5	48.6	53.6	36.0	43
1974-75	Aerial	315	25.6	55.1	19.3	46.0	35.1	24.0	50
1975-76	Aerial	323	15.5	57.6	26.9	26.9	36.9	28	
1976-77	Aerial	258	17.4	57.4	25.2	30.4	43.9	33.6	40
1977-78	Aerial	322	10.9	58.7	30.4	18.5	51.9	43.8	48
1978-79	Aerial	501	13.2	42.3	44.5	31.1	105.2	80.2	55
1979-80	Aerial	675	11.3	41.0	47.7	27.4	116.2	91.2	54
1980-81	Aerial	850	12.5	45.8	41.8	27.2	91.3	71.7	64
1981-82	Aerial	1055	11.9	49.3	38.8	24.2	78.7	63.3	64
1982-83	Aerial	931	10.5	49.1	40.4	21.4	82.3	67.7	46
1983-84	Aerial	1221	16.1	50.0	33.9	32.3	67.9	51.3	65
1984-85	Aerial	947	16.9	61.9	21.2	27.3	34.3	26.9	39
1985-86	Aerial	756	12.2	68.1	19.7	17.9	28.9	24.5	19
1986-87	Aerial	957	6.8	52.7	40.5	12.9	77.0	68.2	51
1960-87	MEAN		16.0	51.9	32.1	30.9	64.6	49.6	49

[a] Cumulative observations on area during December.
[b] All aerial observations by helicopter except 1969-70 (fixed-wing aircraft).
[c] Only west half of area surveyed in 1967-68.
[d] No observations on the study area, NCRCA = adjacent study area.
[e] Survey during February.

through May during all years. The variable recruitment rates to autumn, early winter, and spring for fawns (Tables 4.1, 4.2, and 4.3) resulted in considerable variation in the proportion of fawns in the population during any season or year.

Fawn:female ratios at birth pulse averaged 127:100 and ranged from 99 to 148 fawns:100 females during 1975-1986. There was an average of 74 fawns:100 females during autumn, but ratios varied considerably from 31 to 120 fawns:100 females. During early winter, the average ratio dropped to 65 fawns:100 females, within a range of 29-116 fawns:100 females (Fig. 4.8). In spring, the average was 39 fawns:100 adult deer and the range was 5 to 82 fawns:100 adults. Conversion of these data to fawn:100 female ratios, based on estimated numbers of males in spring populations, yielded an average of 50 fawns:100 females with a range of 6 to 103 fawns:100 females.

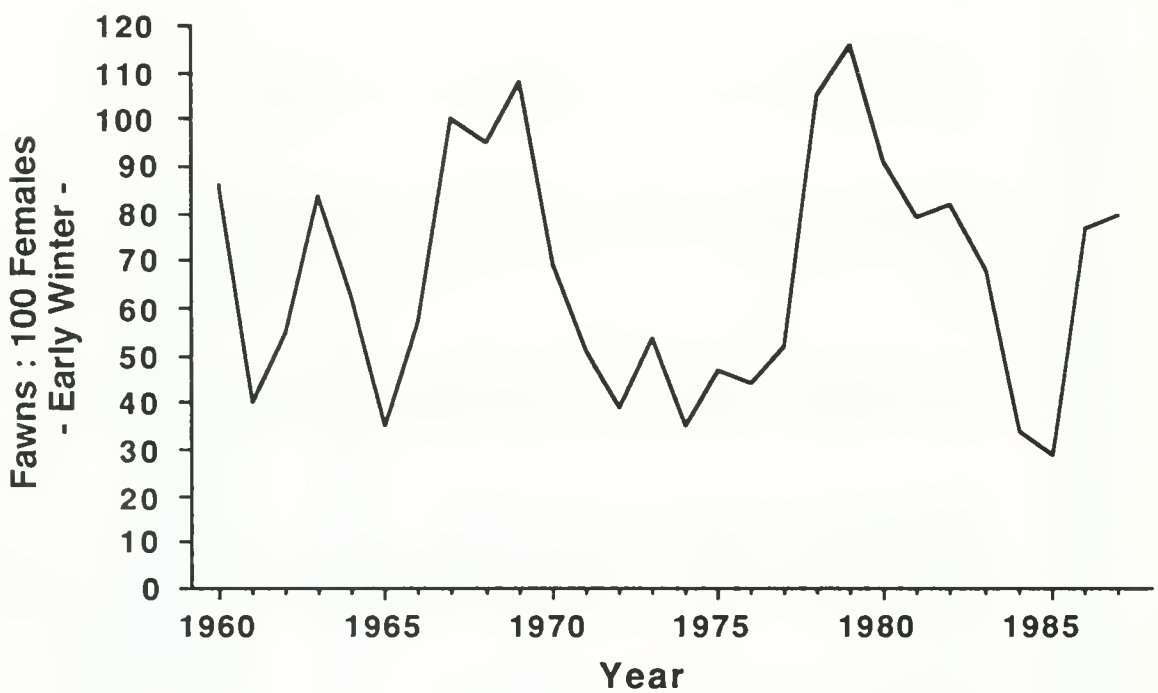


Figure 4.8. Fawns:100 females during early winter, 1960-1987.

Table 4.3. Mule deer population composition during spring, as determined from ground and aerial surveys, 1961-1987, Missouri River Breaks study area.

Year	Type of Observation	Number Classified	Percentage Adults	Percentage Fawns	Fawns:100 Adults
1961	Ground	378	58.7	41.3	70.3
1962	Ground	289	74.7	25.3	33.8
1963	Ground	177	72.3	27.7	38.3
1964	Ground	57	68.4	31.6	46.2
1972	Ground	66	89.4	10.6	11.9
1973	Aerial	235	80.9	19.1	23.7
1976	Aerial	192	90.1	9.9	11.0
1977	Aerial	293	76.8	23.2	30.2
1978	Aerial	246	79.3	20.7	26.2
1979	Aerial	409	60.6	39.4	64.9
1980	Aerial	683	54.9	45.1	82.1
1981	Aerial	738	62.1	37.9	61.1
1982	Aerial[a]	869	65.6	34.4	52.5
	Aerial[b]	295	69.5	30.5	43.9
1983	Aerial[a]	694	62.1	37.9	61.0
	Aerial[b]	488	62.9	37.1	59.0
1984	Aerial[a]	846	80.3	19.7	19.7
	Aerial[c]	122	88.5	11.5	13.0
1985	Aerial	643	95.0	5.0	5.2
1986	Aerial	566	85.0	15.0	17.7
1987	Aerial	861	60.7	39.3	64.6
1961-1987	Mean		73.9	26.1	39.1

[a] March
[b] April
[c] May

Adult Females

Data on the age structure of adult female populations were available from deer killed by hunters for 1960-64 and from hunter-kills and winter trapping during 1978-1985 (Table 4.4). Age distribution among deer killed by hunters may not have been representative of the population age structure because some age-classes of females, especially yearlings and the oldest females, appeared to be harvested at higher rates than others (see Chapter 6). Nevertheless, these data, if not mathematically reconcilable from age-class to age-class, appeared to represent the general changes in age structure.

Table 4.4. Adult female age structure from hunter-killed and captured mule deer, expressed as percentages in each age class.

Year	N	Age in Years 1	2	3 - 6	7 +
1960	46	22	13	28	37
1961	63	21	8	54	17
1962	35	11	31	37	20
1963	10	10	20	40	30
1964	19	32	21	37	11
1960-64	173	20	16	41	23
1978	33	21	24	36	18
1979	10	40	0	50	10
1980	17	29	6	47	18
1981	55	20	29	35	17
1978-81	115	23	22	38	17
1982	55	33	29	33	6
1983	49	31	16	42	10
1984	47	13	34	40	12
1985	27	4	0	85	11
Mean	13 years	22	18	43	17

For example, yearlings were relatively poorly represented in the population during autumn 1962 and 1963 (Table 4.4) as expected based on relatively poor fawn recruitment during 1961 and 1962 as compared with 1960 and 1963. Poor recruitment of the 1983 and 1984 cohorts was also indicated by the hunter-killed samples (Table 4.4).

There was little difference in age structure for a period of high harvest rates for females (1960-1964) and a period of no harvest of females (1978-1981, Table 4.4). Females had not been legally harvested for 6 years prior to autumn 1981. The period of 1978-1981 was a time of population growth and young deer were well represented in the population.

Modeled estimates of age structure each year from 1968 through 1986 are shown in Fig. 4.9. The model added the number of fawns recruited from each cohort starting with 1960, and annually reduced those numbers based on estimates of hunting and winter losses and dispersal, before advancing it to the next age class. Age-specific differences in mortality (Chapter 6) were also considered. For years when data were

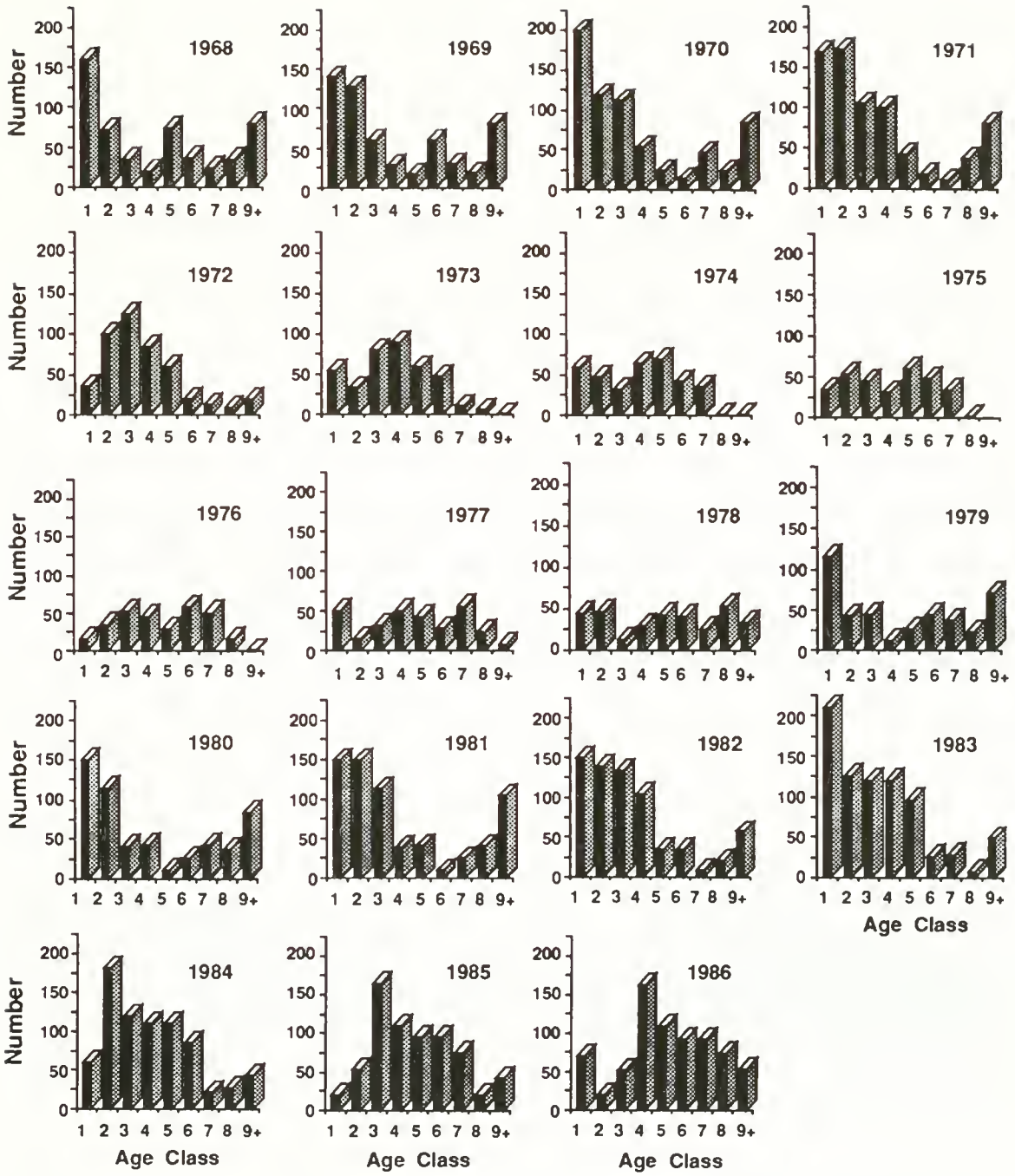


Figure 4.9. Modeled age structure of the female population during spring, 1968-1986. Age class 1 is 12 month-old females.

also available from trapping and hunter-killed samples, we considered the modeled estimates more accurate than those derived from small samples of trapped and hunter-killed deer. Given those small samples, randomness, hunter selection, and misaging could significantly influence proportions assigned to each age class. The general form and structure of the 2 estimates was similar, though age-specific differences appear (Fig. 4.10). Both generally detected cohorts with poor survival (1971, 1975, 1983, and 1984).

The general age structure of the population was the same during 2 different periods of population increase, 1968-1971 and 1979-1983 (Fig. 4.9). Age structure was also similar for 2 periods of decline, 1972-1974 and 1984-1986. The major difference was that the population decline during 1972-1974 was more severe and population size was lower than during 1984-1986. Continued low fawn recruitment during 1975-1977 further reduced population size and perpetuated the small base in female age structure during the earlier decline.

It is apparent from age structural estimates (Fig. 4.9 and Table 4.4) that age structure alone is not a useful criterion for predicting future population trends. Rather, it was most useful for determining or verifying what had happened in the past. Used alone, or with invalid assumptions, age structural data may be potentially misleading in determining population trend. Population declines during both 1971-72 and 1983-84 were preceded by several years in which the pyramidal age structure represented the classic, "healthy and growing" population. Both declines were represented by sharp, rather than gradual deviations from this age structure.

A stable age structure cannot be expected for this population. Persistence of a "normal" or "stable" age structure requires relatively constant natality and mortality. On our study area, natality and mortality of fawns occurred as periods of several years of both boom and bust. Hunting mortality was variable. Although natural mortality of adults appeared relatively stable during most years, it occasionally occurred as a pulse of catastrophic mortality. The greatest age structural stability occurred from spring 1975 through spring 1978 (Fig. 4.9), when fawn survival was low, but relatively stable, and adult female mortality was low and stable.

Only 16.5% of 466 adult females aged during 1960-1985 were 7 years or older; 40% were yearlings or 2-years-old. The maximum age recorded for females was 16 1/2 years.

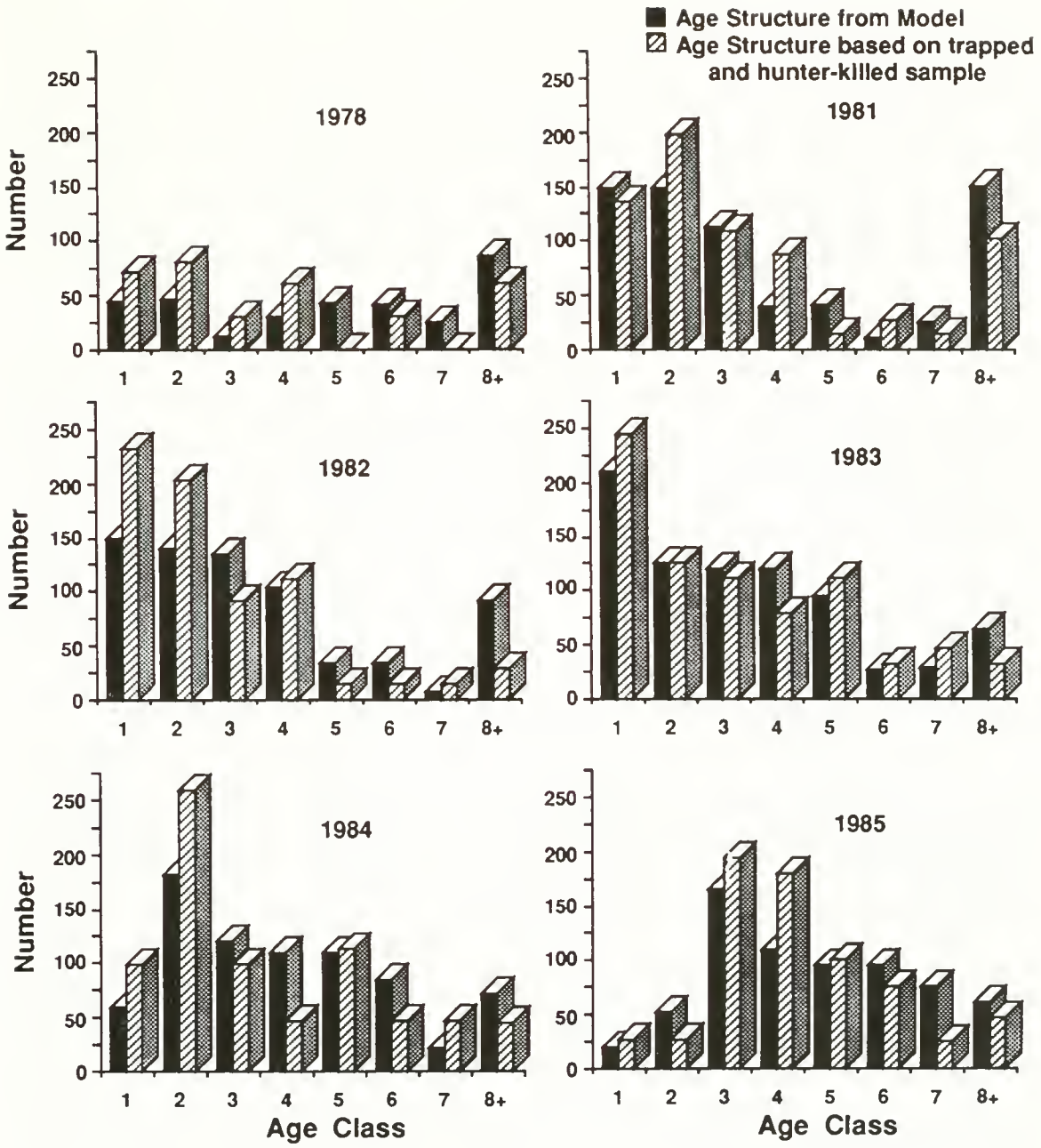


Figure 4.10. A comparison during six years of female age structure based on the modeled estimate with female age structure based on a sample of trapped and hunter-killed deer.

Adult Males

Information on the age structure of adult male populations was provided by deer killed by hunters during 1960-1964 and 1976-1986 (Table 4.5). Male age structure and changes were also estimated using the model that added in each recruited cohort, starting with 1960, and reduced its numbers on the basis of annual and average estimates of hunting and winter losses (Fig. 4.11). Age-specific differences in mortality were applied to 3 age classes: yearlings, 2-year-olds, and 3-year-old and older males, based on mortality data from 1976-1986 (Chapter 6). Data were also available to age males as either yearlings or older adults from aerial classifications during 1976-1986 (Table 4.6).

The 3 estimates of male age structure generally followed the same trend, though some differences were apparent (Table 4.6). Aerial classifications usually over-estimated yearling males as compared to estimates based on fawn recruitment. That probably occurred because, from the air, some small-antlered, 2-year-old males were misclassified as yearlings. The proportion of yearling males in the harvested sample was lower than estimates based on fawn recruitment. That was also expected because age-specific mortality data indicated that yearling males were harvested at a lower rate than older and larger males. Because those 2 estimates deviated as expected from the estimate based on fawn recruitment, we considered the estimates based on fawn recruitment to be the most accurate.

Although age structures for harvested males, 1960-1964 and 1976-1986 (Table 4.5), probably underestimated proportions of yearling males and overestimated older males in the population, they did indicate the numerical importance of yearling males to the total harvest, even during years following poor fawn recruitment. The modeled age structure (Fig. 4.11) also indicated the importance of yearling males to the surviving male population. Because the total male population after the hunting season was usually one-third or less that of the female population, the size of each annual cohort had a proportionately greater effect on numbers of males in the population than on female numbers (Figs. 4.9 and 4.11). As a result of hunter selection for older, larger-antlered males, the male age structure generally retained a more pyramidal shape than that for females, even at low population levels following poor fawn recruitment (Figs. 4.9 and 4.11). Harvest rates of males that averaged over 40% reduced the influence of strong year classes much sooner than occurred among the female population.

Only 3.4% of 739 adult males aged during 1960-1986 were 7 years or older. Seventy percent (70%) were yearlings or 2 years old. The oldest male was 11 1/2 years-old.

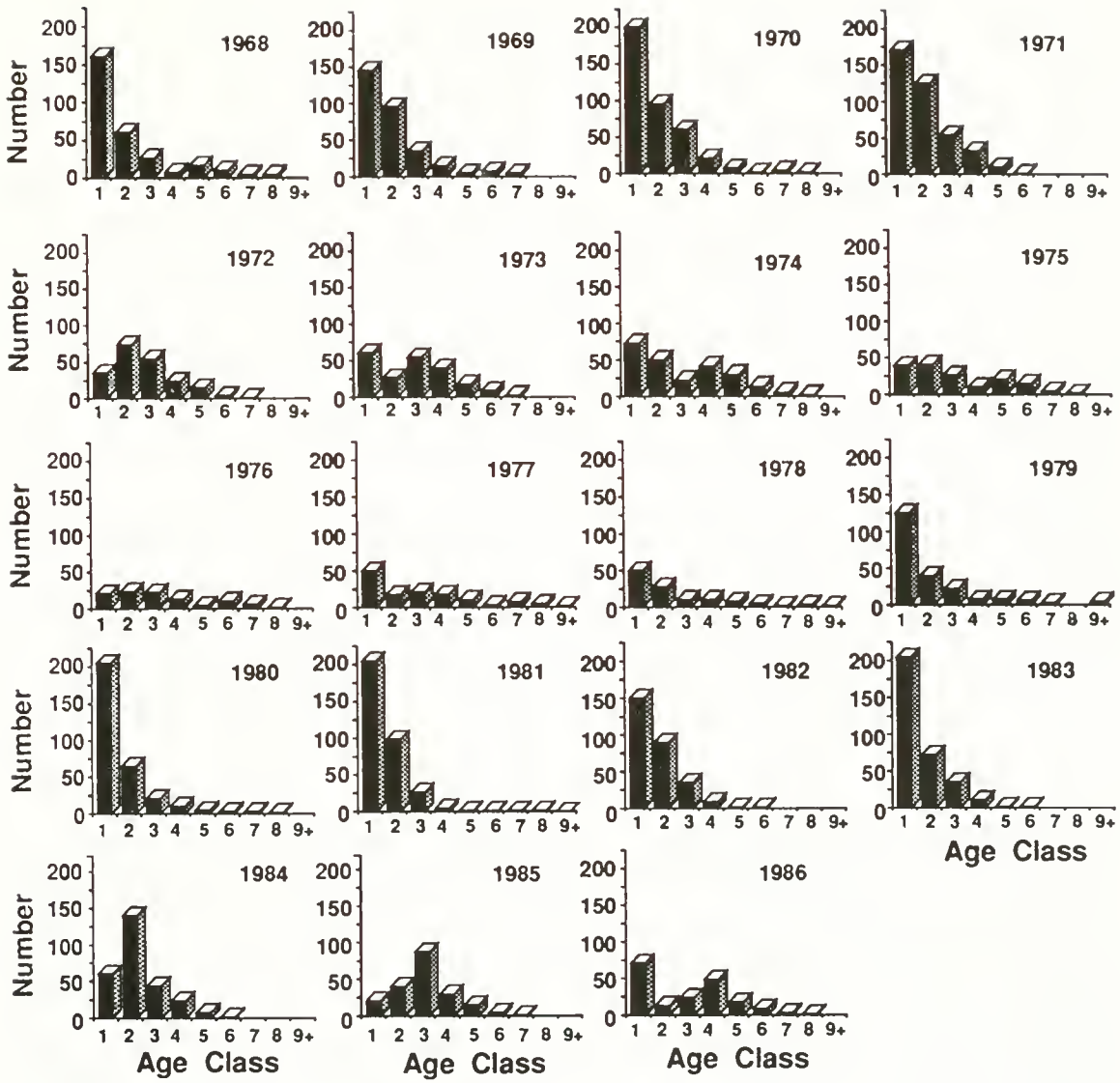


Figure 4.11. Modeled age structure of the male population during spring, 1968-1986.

Table 4.5. Adult male age structure from hunter-killed deer, expressed as percentages in each age class.

Year	N	Age in Years 1	2	3 - 6	7 +
1960	73	53	18	21	8
1961	66	59	14	20	8
1962	31	42	48	10	0
1963	16	50	19	31	0
1964	43	47	16	30	7
1976	16	50	25	25	0
1977	21	38	14	39	9
1978	11	18	31	51	0
1979	29	52	27	21	0
1980	71	54	21	22	3
1981	102	49	36	11	4
1982	54	41	36	23	0
1983	95	55	17	27	1
1984	49	22	39	39	0
1985	16	0	19	75	6
1986	46	20	20	58	2
Mean	16 years	41	25	31	3

Table 4.6. Percentage of yearling mule deer in the male segment of the population during autumn as determined by three methods, 1976-1986.

Year	Method: Spring Population Estimates	Autumn Aerial Classifications	Hunter Harvest
1976	20	39 (31)[a]	50 (16)[a]
1977	39	41 (20)	38 (21)
1978	44	52 (33)	18 (11)
1979	58	65 (57)	52 (29)
1980	66	62 (139)	54 (71)
1981	59	55 (151)	49 (102)
1982	53	63 (96)	41 (54)
1983	63	67 (146)	55 (95)
1984	21	32 (107)	22 (49)
1985	10	10 (61)	0 (16)
1986	38	29 (42)	20 (46)
Mean	43	47	36

[a] Number in parenthesis is the sample size.

Mule Deer Condition

Antler Characteristics

Antler characteristics, especially of yearling males, have been related to nutritional qualities of the diet and physical condition in deer (French et al. 1956, McEwen et al. 1957, Robinette et al. 1973, and Rasmussen 1985). Generally, antler size as expressed by total weight, beam diameter, number of points, and beam length increases with nutritional plane.

Antler characteristics of mule deer on our study area (Table 4.7) indicated that yearling males were in relatively poor condition during 1961, 1970, 1984, and 1985. They also may have been in relatively poor condition during 1964. Better than average condition was apparent for 1963, 1974, 1978, 1979, and 1987. Data for other years either indicated average condition or conflicting conclusions were given by beam diameter and antler point measurements.

Although antler measurements did not exactly reflect overall deer herd performance in all years, they accurately reflected forage conditions and fawn survival during years when antler measurements were at extremes in either direction. Because antler measurements may also be affected by conditions prevailing at birth, genetic factors, hunter selection, and stocastity, "noise" may mask changes resulting from nutritional status during years of less than extreme condition.

Weights

Relative deer weights by sex and age class have also been considered an indicator of nutritional status (McEwen et al. 1957 and Klein 1970). Limited data on deer weights recorded during some years of the study (Table 4.8) verified that all deer were in relatively poor condition during 1961 and 1984. During 1962, the weights of yearling and 2-year-old males as well as 2-year-old-and-older females were above average despite poor fawn survival. Weights of adult females were probably above average that year because few females recruited fawns to autumn during either 1961 or 1962 and, relieved of lactation stress and with good forage conditions after June, most females recovered body condition by autumn 1962.

Weights of adult females were usually below or near average during years of drought and/or during years following several years of above average fawn recruitment. For example, antler beam diameter (Table 4.7) and weights of yearling males (Table 4.8) were above average during 1981, but weights of adult females were slightly below average after having

Table 4.7. Antler characteristics for mule deer on the Missouri River Breaks study area, 1960-1984.

	Beam diameter (mm) 2.54 cm above burr				Antler points per side						
					1-1/2 Males					2-1/2 Males	
Year	N	1 Males	N	2 Males	N	Harvest	N	Post Season Survey	% 2X2 or Greater	N	Harvest
1960	42	16.8(2.8)[a]	11	24.5(2.6)[a]	44	1.84	37	1.72	62	14	3.21
1961	35	14.9(2.3)	10	22.2(1.6)	41	1.50	46	1.50	48	12	2.88
1962	12	16.6(1.8)	9	25.3(3.4)	13	1.77	20	1.98	85	10	3.00
1963	9	19.1(3.1)	3	25.5(1.2)	9	2.06	25	1.86	84		
1964	22	16.8(1.7)	15	23.8(2.1)	28	1.89	63	1.62	62	16	2.81
1965							31	1.76	74		
1966							25	1.80	68		
1970							70	1.50	41		
1971							59	1.80	68		
1973							39	1.76	72		
1974							39	1.87	82		
1975	15	19.6(1.6)[b]					13	1.65	62		
1976	6	17.5(1.7)			7	1.86	20	1.83	65		
1977	8	17.9(1.0)			8	1.94	15	1.73	75		
1978	3	18.8(0.6)	7	24.6(1.4)[c]	4	2.00	33	1.86	83	7	3.43[c]
1979	12	19.6(2.5)			14	2.21	39	1.92	83		
1980	36	17.4(1.6)	14	24.4(2.2)	36	1.99	67	1.82	73	14	3.07
1981	45	19.1(2.6)	20	25.3(2.7)	50	1.97	80	1.73	56	20	3.25
1982	17	17.7(1.8)	7	24.5(1.5)	17	1.91	45	1.86	78	10	2.90
1983	31	18.6(1.9)	10	25.6(1.9)	32	2.02	125	1.81	72	12	3.58
1984	11	16.8(1.7)	11	23.5(2.0)	11	1.68	63	1.47	40	11	3.27
1985			4	25.0(3.0)			18	1.37	28	4	2.71
1986	7	18.4(1.8)	7	25.5(3.6)	7	2.21	33	1.66	55	7	3.14
1987					44	2.03					
Mean		17.9(1.3)		24.6(1.0)		1.93		1.73	66		3.10

[a] $\bar{X}$ beam diameter (std. deviation)
[b] data from South Phillips County (NCRCA)
[c] 1978 and 1979 combined

Table 4.8. Autumn weights (kg) of mule deer from the Missouri River Breaks area, 1960-1987.

Year	Males			1 Males			2 Males			Females			1 Females			2 + Females		
	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD
1960	6	24.1	1.3	30	44.4	4.2	8	58.3	3.1	15	21.5	1.6	6	36.2	2.3	30	44.9	3.9
1961	6	21.3	1.2	27	39.9	5.8	6	57.7	3.6	7	20.6	2.5	8	37.6	3.8	17	41.5	5.5
1962	3	23.7	0.7	9	47.9	3.6	7	60.1	3.7				3	37.1	0.7	13	47.9	2.5
1963	6	21.9	1.5	8	42.7	5.1	3	53.4	3.0	3	20.1	1.8				8	42.5	4.1
1964	8	23.8	1.4	19	43.6	3.8	14	58.5	4.6	4	22.2	2.3	13	37.8	4.6	26	44.7	2.9
1965	3	22.1	3.1				4	60.3	4.7				3	36.6	0.3	6	44.8	3.4
1975[a]				9	39.9	3.4												
1976				5	41.3	5.2												
1981	3	25.1	1.5	9	45.0	6.5				4	23.9	3.8				3	42.5	0.7
1982										4	24.9	1.9						
1983	4	22.9	1.0	16	41.1	3.6	3	58.6	1.4	3	21.6	1.1						
1984				4	38.7	3.6	6	49.4	5.9	4	19.2	2.5	4	34.6	2.4	11	42.0	3.9
1985							2	55.1	8.7							2	44.2	4.8
1986				4	43.9	3.8	2	51.9	2.9									
1987				39	45.1	4.7	8	58.7	7.6				4	40.9	2.9	16	42.0	4.4
Mean		23.1	1.3		42.8	2.7		56.5	3.6		21.8	1.9		37.3	1.9		43.7	2.0

[a] Data from south Phillips County (NCRCA).

recruited fawns at above average rates during 2 prior drought years. Similarly, weights and antler characteristics of both yearling and 2-year-old males were above average during autumn 1987, but weights of adult females were below average after 2 years of above average fawn recruitment. Yearling females had not undergone lactation stress and were above average in weight during 1987.

Percent Femur Marrow Fat and Kidney Fat Index

Percent femur marrow fat (FMF) and a kidney fat index (KFI) can indicate physical condition in ungulates, especially when both measurements are recorded (Riney 1955 and Ransom 1965). We collected consistent data on FMF and KFI only from December 1983 through December 1985, when deer were in the poorest condition of recent times (Table 4.9). As reported by Ransom (1965), significant utilization of FMF did not begin during winter 1983-84 until the kidney fat index declined below about 30. Fat reserves of deer declined over winter 1983-84, as would be expected, but deer were in relatively better condition during that winter of high mortality than during the winter of 1984-85 when mortality was less than or equal to that during winter 1983-84. Average FMF levels for adult females collected during March 1985 were 41% below those for adult females collected during March 1984, but mortality rates of fawns and adults were nearly the same during the 2 winters.

Table 4.9. Average kidney fat indexes (KFI) and average percentage femur marrow fat (FMF) for adult female mule deer collected or shot by hunters in the Missouri River Breaks, 1983-1985.

	KFI				FMF			
Date	N	$\bar{X}$	SD	Range	N	$\bar{X}$	SD	Range
12-83	3	50.9	62.0	26-122	3	91.7	2.4	89-93
02-84	9	21.3	13.2	13-55	9	81.8	6.4	70-91
03-84	6	16.5	10.5	9-37	6	72.3	15.7	51-86
11-84	6	31.8	11.7	11-47				
03-85	5	7.6	2.6	6-12	5	33.6	20.4	11-53
04-85	5	13.2	5.0	6-20	5	29.6	19.4	10-56
11&12-85	5	80.8	61.2	11-170	2	95.0	1.4	94-96

Four of 10 adult females collected during March and April 1985 had FMF levels (10-12%) equivalent to 3 deer from adjacent areas that were known to have died of malnutrition during winter (7-11%). Femur marrow fat levels indicated that 40% of females collected during March were in very poor

condition, however only 3 (7%) of 44 marked adult females died after March. Thus it seems likely that mule deer can recover from FMF levels near 10-12% if new succulent forage becomes available by late March. Deer were in very poor condition during winter 1983-84 and especially 1984-85, but more than 90% of the adult females survived the winter of 1984-85, when "green-up" occurred early, regardless of condition or coyote predation.

The physical condition of female mule deer during late March and April undoubtedly depended on their reproductive status. The 3 females collected during December 1983 (Table 4.9) were all radio-collared females with known reproductive histories. The female that had either not had fawns or lost them immediately after birth had a KFI of 122. The other 2 females, both accompanied by fawns at the time of collection, had KFIs of 26 and 25. All 3 had FMF values above 89%. This supported our speculation that females which have not experienced long periods of lactation stress weigh more than those that recruit fawns during consecutive years.

Only color and consistency of marrow samples were recorded during 1975-76. However, comparison of color and consistency with percent FMF in subsequent samples made general estimates of percentage of FMF possible. Femur marrow samples from a fawn and an adult mule deer of unknown sex killed by coyotes during mid-January 1976 were both categorized as white and firm. Twenty-one samples of femur marrow subsequently classified as white and firm averaged 84% FMF (range, 70-96%). A yearling male killed by coyotes on 30 January 1976; an adult of unknown sex killed on 5 March 1976; and a 3-year old female killed on 6 March 1976 all had femur marrow classified as yellow and soft. Twelve femur marrow samples subsequently classified as yellow and soft averaged 50% FMF (range 36-62%). The femur marrows of 2 other mule deer killed by coyotes in late winter 1976 were classified as red and viscous, which in subsequent samples ranged from 7-19% FMF.

An adult female killed by coyotes during February 1977 and 2 adult females that died as the result of capture and marking operations during February and March 1977 all had FMF levels above 90%. A fawn killed by coyotes in 27 February 1978 had a FMF level of 90%, another killed on 7 March 1978 had a FMF level of 43%.

In combination with antler measurements and deer weights, these data indicated that mule deer were apparently in better physical condition during winters 1975-76 through 1977-78 than during those of 1983-1985 (Tables 4.7, 4.8, and 4.9). Fawn mortality was high during both periods.

Age and Condition of Coyote-killed Deer

During winters, 1975-1986, 149 deer carcasses, including radio-collared deer, were examined and classified as coyote-killed deer. These included 118 mule deer and 31 white-tailed deer from the adjacent river bottoms. Very little remained of most carcasses, and 76 (58 mule deer and 18 white-tailed deer) were of unknown sex and age. Because of the small size of fawns and their relatively higher rate of disappearance over winter, it is likely that many of the unknown sex and age carcasses were fawns. Of the remainder, 34 were adult mule deer, 26 were fawn mule deer, 10 were adult white-tailed deer, and 3 were fawn white-tailed deer. For adults classified to sex, 20 mule deer and 8 white-tailed deer were adult females and 2 mule deer were adult males. Of the 30 adults of both species and sexes aged to specific age, 9 (30%) were yearlings, 15 (50%) were between 2 and 8 years of age, and 6 (20%) were 8 years old or older. This small sample did not indicate that coyotes selectively killed adult deer in different age categories than occurred over long periods in hunter-killed and captured samples of female deer (Table 4.4).

Estimates of FMF content for coyote-killed deer ranged from 70-96% for 14 deer, 32-62% for 10 deer, and 7-17% for 8 deer examined over 10 years. Deer in relatively poorer condition did not prevail in this sample.

Fat content of femur marrow is not enough, by itself, to determine deer condition (Mech and Delgiudice 1985). For example, deer with FMF content in the range of 70-96% (white and firm) could either be in excellent condition or on the verge of protein catabolism and starting to utilize critical body fat reserves. In northern environments, fat reserves and body condition of deer usually decline over winter (Anderson et al. 1974, Mautz 1978), even in areas where deer are on a relatively high nutritional plane during the period (Dusek et al. 1989).

Timing is also important; deer with FMF content of 40% in January are in worse condition than those with FMF content of 40% in March. As indicated earlier, most females with a FMF content below 20% during March and April 1985 apparently survived winter and recovered to recruit fawns during 1986 and 1987. Of 32 marrow samples from coyote-killed deer, only about 7 were considered in such poor condition at the time of death that over-winter survival was unlikely. We do not mean to imply that the remainder of deer killed by coyotes were in excellent or good condition, only that they fell within the "normal" range of conditions for deer at the time of the year they died. The FMF content of 2 fawns and 3 adults killed by coyotes during February and March 1977-80 was considered to be excellent and above "normal" for that time of year.

Deer in poor condition undoubtedly were more vulnerable to coyote predation than deer in relatively good condition. Our data were not sufficient to indicate the relative degree of selection by coyotes for deer in poor condition over other deer. However, because more deer, both fawns and adults, generally died during winters when deer were in relatively poor condition, some selection must have occurred.

Circumstances and site conditions were also indicated to play a role in predation such that relatively high numbers of "healthy" deer were killed by coyotes during years such as 1975-1978. The situation referred to earlier, where 1 fawn killed by coyotes on 7 March 1978 had a FMF content of 43% while another fawn killed 1 week earlier, on 27 February 1978 had a FMF content of 90% indicated that relative condition of the deer was not always the overriding factor determining predation rates. Both of these fawns, as well as a whitetail fawn killed on 7 March 1978 (72% FMF), had FMF contents equal to or higher, for the same time of year, as most of the adult female population during winters 1983-84 and 1984-85. Relatively high mortality owing to coyote predation on this area did not necessarily mean that deer were in poor condition or that most of those killed by coyotes would not have survived winter.

Deer condition fluctuated throughout the period 1960-1987. Combined evidence from antler measurements, weights, fat indexes, and fawn birth dates (see Chapter 5) indicated that deer were in better than average condition during late 1962 and early 1963, 1978, 1979, and 1987. Deer were in poorer than average condition during 1961, 1984, and 1985. More limited evidence suggested that deer may have also been in relatively good condition during 1986 and relatively poor condition during 1964 and 1970. The available data also indicated that deer were in average or above-average condition during 1973-1975 when fawn mortality was high.

The condition of adult females did not always coincide with the condition of adult males. Cumulative reproductive and lactation stress was apparently such that after several years of recruiting above average number of fawns, female condition declined even if forage condition were relatively good. Female condition recovered (1962, 1985) after 1 or 2 summers when few fawns were recruited. Even with relatively stable forage conditions, it is unlikely that females can sustain high rates of fawn recruitment while maintaining good body condition and high survival.

Deer killed by coyotes during winter were not necessarily in poorer condition than their cohorts during the same year or in other years. At least some deer killed by coyotes were in better condition than survivors during other years.

CHAPTER 5

REPRODUCTION AND FAWN MORTALITY

Conception and Birth Dates

Conception dates were calculated from fetal measurements (Hudson and Browman 1959) for 32 litters; 9 from 1962-63, 14 from 1984-85, and 9 from 1985-86. Those data indicated conception occurred from 15 November to 24 December with a median date of 25 November. Seventy-five percent of litters were conceived between 21 November and 1 December. Based on a mean gestation period of 203 days (Robinette et al. 1973), births would have occurred from 6 June to 15 July, with a median of 16 June. These dates appear somewhat late for conception and parturition, based on other data and observations. Most fetuses were collected during 1984 and 1985, when deer were generally in poor condition and conception and parturition may have occurred later than average. Newborn fawns were observed as early as 2 June, 4 days prior to the earliest date projected by fetal measurements.

Birth dates calculated from the weights of fawns captured during June (Robinette et al. 1973) were earlier than those projected from fetal measurements. Few of the fawns were newborn, and most were at least several days old; weights ranged from 2.7 kg to 9.3 kg ($\bar{X}$ = 5.4, SD=1.4, n=194). Birth dates calculated by this method project only the early end of the range because fawns were born after capture operations ceased. The earliest was 27 May and 33 (23%) of 146 litters were born prior to 6 June. Considering all data, we estimate parturition to occur between 27 May and July 15, with a median of 10-12 June. The corresponding median date of conception was 20-22 November.

Although the general time of breeding and conception is probably established by photoperiodism (Verme and Ullrey 1984), dates of conception within any local area may be influenced by nutrition and age, among other factors (Verme 1965 and Robinette et al. 1973). Both Verme (1965) and Robinette et al. (1973) indicated that well nourished females gave birth earlier and/or had a shorter gestation period than females on a lower nutritional plane. The effect of the dam's nutritional status on birth weights of fawns is not clear (Verme 1965 and 1969, Murphy and Coates 1966, and Robinette et al. 1973). Available evidence suggests that a threshold birth weight may exist, and within limits, the gestation period is longer and fetuses are smaller among females on a lower nutritional plane.

In examining possible effects of nutrition on the reproductive period of deer on our study area, we assumed that birth date was most likely to vary with nutritional plane of the female. Birth dates of fawns captured during 1977-1987 were estimated from the equations of Robinette et al. (1973) unless known to have been the day of capture. Data for 1976 were excluded because capture operations started later than in all other years. Capture dates during 1977-1987 ranged from 12 June to 28 June and averaged 16 June. Only fawns estimated to have been born by 14 June each year were used for 1 comparison, while all fawns captured were used for another. Although fawns born only during the early portion of parturition were included, the means and ranges in birth dates should indicate relative differences among years.

Mean birth dates (Fig. 5.1) represent conditions prevailing from summer prior to conception through late winter before birth. Thus, conclusions drawn about birth weight during a particular year apply to nutritional conditions during the year prior to birth. If early birth dates were related to superior female condition, nutritional conditions prevailing from summer 1978 through spring 1979 and from summer 1986 through spring 1987 must have been far above average, verifying other data (Chapter 4). The first period coincided with very low deer density, the second with very high deer density. The worst nutritional conditions must have occurred from summer 1983 though winter 1984. Conditions during summer 1981 through spring 1982 and summer 1976 through spring 1977 may also have been poorer than average.

Although average birth dates indicated that nutritional conditions were near average during 1984-1985, that interpretation must be tempered by the information on low pregnancy rates of females during those years. Because about 20% and 17% of 2-year-old and older females were either not carrying viable fetuses or had late births in 1984 and 1985, nutritional conditions probably were poorer than indicated by average birth date alone. Those females that gave birth to viable fawns may have been in average condition, but when balanced with the other females, the female population as a whole was in poorer than average condition.

Poor nutritional conditions may also have prevailed during 1982-1983. Ten late-born fawns were observed during the course of late summer and autumn fieldwork in 1983. The highest number observed during any other year was 2.

Pregnancy, Ovulation, and Fertilization Rates

Pregnancy rates were determined from females shot for that purpose and from observations of marked females. Data from 39 1-1/2-year-old and older females collected in the

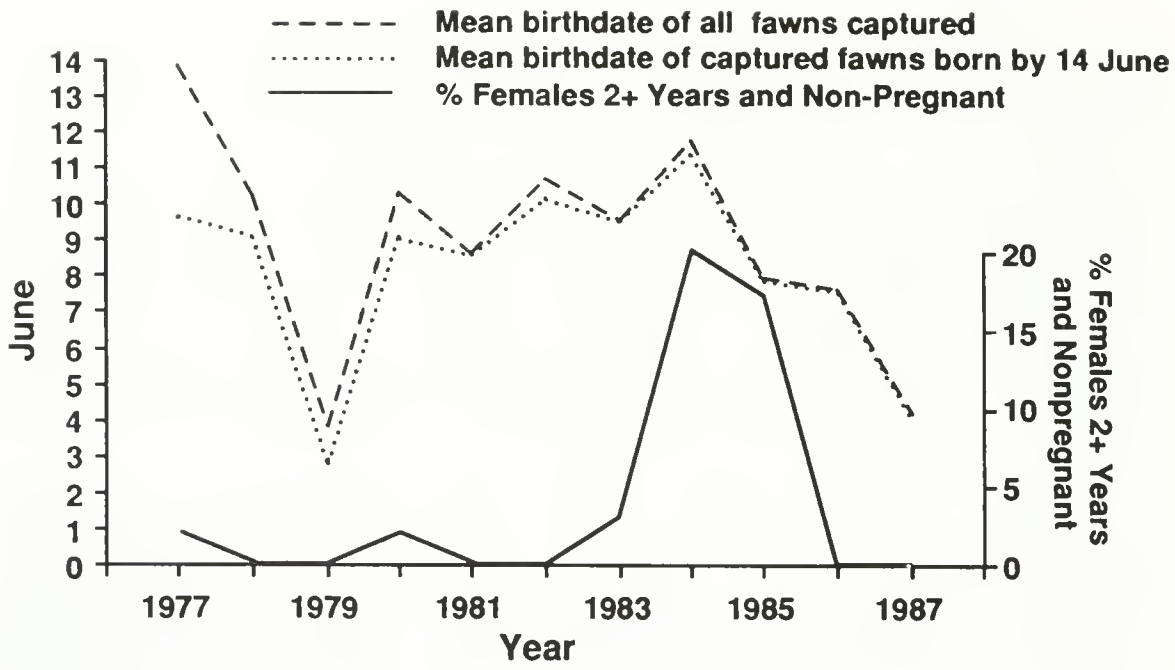


Figure 5.1. Mean birthdate for captured mule deer fawns and % of females 2 years or older that were not pregnant during 1977-1987 in the Missouri River Breaks, Montana.

Missouri River Breaks during 1958, 1963, 1984, and 1985 indicated that 38 (97%) were pregnant. Pregnancy rates were high even though 25 of the 39 females were collected during 1984 and 1985 when fawn survival after birth was very poor. The 1 non-pregnant female, a yearling, was collected in spring 1985.

Pregnancy rate as determined by observation of marked females during 1976-1983 was 91% (177 of 194). This method somewhat underestimated pregnancy rates because females abandoning or losing fawns within a few days of birth could have been classified as non-pregnant. Regardless of the source of data, apparently more than 90% of female mule deer in this area conceived successfully. That was higher than the 85% pregnancy rate recorded for 129 adult females examined statewide during 1975-1979 (Pac 1979).

Ovulation rate for 35 adult females collected during 1963, 1984, and 1985 was 1.66 ova per female or 1.71 per pregnant female. Fertilization rate for ova in females collected during spring 1963 was 100% (16 of 16). Fertilization rates for ova during 1984 and 1985 were 82% (22 of 27) and 92% (12 of 13), respectively. The 89%

fertilization rate for the entire sample was comparable to the 92% rate recorded for the statewide sample (Pac 1979).

Fetal rate during 1984 was 1.47 fetuses per pregnant female (15 females - 22 fetuses) and fawn-at-heel ratio at parturition was 1.39 fawns:female. For 1985, fetal rate was 1.33 fetuses:pregnant female (9 females - 12 fetuses) and fawn-at-heel ratio at parturition was 1.25 fawns:female. Those data indicated an in-utero loss of 5.4% and 6.0% in litter size between March and parturition for 1984 and 1985, respectively.

There must have been high rates of late gestation abortion or resorption, early neonatal abandonment, and/or late births during 1984 and 1985. Two of 19 fawns radio-collared during June 1984 were abandoned by their mothers after birth. Both were the smaller member of sets of twins; the larger twin, also handled and marked, was not abandoned in either case. All 15 females collected in February and March 1984 were pregnant. As determined by behavior, social grouping, and appearance, 28% of females were classified as non-pregnant during mid-June 1984. Only 8% of all females on the area were too young to have bred. Although 9 of 10 females collected during March and April 1985 were pregnant, 21% of all females were classified as non-pregnant in mid-June when only 3% were too young to have bred.

The following scenario was indicated for females under increasing nutritional stress. Initially, almost all breed and become pregnant. Ova were shed at near normal rates, but substantial numbers were not fertilized (18%+ in 1984). A relatively small loss in average litter size occurred *in utero* (5.4% in 1984 and 6.0% in 1985). A major loss of fawns occurred as females aborted their fetuses shortly before parturition or abandoned fawns at or shortly after parturition (20% in 1984 and 17% in 1985). It was also possible that females classified as non-pregnant during mid-June in 1984 and 1985 were pregnant, but had late births. Those females may not have had the appearance of pregnancy or exhibited behavior of parturition by mid-June. If late born fawns died shortly after birth, their occurrence would have been hard to detect.

The only major changes from the scenario during the second year of nutritional stress were that fewer females became pregnant and fewer ova were shed than normal (20% fewer in 1985). The females that did not become pregnant probably were mostly first year breeders and older females in very poor condition. Other patterns of loss in potential production were similar to those of the first year of nutritional stress.

Fawn Production, Mortality, and Recruitment

General Patterns in the Population

1975-1986

Fetal rate for 38 pregnant females collected in spring 1958, 1963, 1984, and 1985 was 1.55 fetuses:female. We consider that rate to be below average because 64% of the sample was from 1984 and 1985, the lowest years of production on record.

Initial production of fawns was also recorded each year during 1976 - 1986 as fawn-at-heel ratios during June (Table 5.1). Those data did not account for females that were not pregnant. They also underestimated initial litter size to some degree because fawn mortality was ongoing at the time the data were collected. Additionally, during 4 of 11 years, a radio-collared fawn originally classified as a single, was later determined to be a twin. Undoubtedly, some non-radio-collared litters included in the sample may have also had an additional fawn. That likelihood was verified by comparing litter size during 1976-1983 between the population as a whole and radio-collared females that were reobserved often. Single fawns comprised 43.8%, twins 54.8%, and triplets 1.4% of 292 litters recorded in initial fawn-at-heel surveys (Table 5.1). Singles were 31.6%, twins 65.6%, and triplets 2.8% of 177 litters for radio-collared females. Most of this difference occurred because reobservations of radio-collared females detected a larger litter size than recorded for the initial observation.

The mean litter size for aggregate data during 1976-1986 was 1.58 fawns per productive female. The highest was 1.76 and the lowest was 1.25 fawns per productive female in 1979 and 1985, respectively. The lowest ratio was 71% of the highest, indicating the range in adjustment of litter size under the extremes in conditions experienced during this period.

During 1979, the year of best production, 73% of litters contained more than 1 fawn. A minimum of 11 sets of triplets were known to have been born, 7 of which survived through December. These 11 sets of triplets represented 3.6% of litters for breeding age females on the study area. The fawn-at-heel ratio recorded in mid-June 1979 (Table 5.1) also may have been lower than the actual ratio at birth.

Fawn-at-heel ratios were multiplied by the percentage of the female population estimated to be productive (see footnotes, Table 5.1) to obtain an estimate of the fawn:female ratio for the population during mid-June. Those ratios were

Table 5.1. Fawn-at-heel ratios during mid-June and estimated percentage of females productive and population fawns:100 females ratio during June.

Year	Females	Litter Size 1	2	3	Fawns: Female	Estimated[a] Percentage of Females Productive	Fawns:100[b] Females for Population
1975[c]	8	3	5	0	1.63	89	145
1976	14	7	7	0	1.50	94	141
1977	20	8	12	0	1.52	82	125
1978	26	9	17	0	1.65	90	148
1979	37	10	26	1	1.76	71	125
1980	22	8	13	1	1.68	75	126
1981	26	11	14	1	1.62	78	126
1982	32	14	18	0	1.56	79	123
1983	32	13	19	0	1.59	71	113
1984	31	20	10	1	1.39	72	100
1985	24	18	6	0	1.25	79	99
1986	28	10	18	0	1.64	90	148
TOTAL[d]	292	128	160	4	1.58		
Percentage		43.8	54.8		1.4		

[a] Three sources of data used:
1) Percentage of female population older than yearling.
2) Percentage of yearlings that emigrated.
3) Percentage of females observed during June that were not with other adult deer.

[b] Numbers in this column obtained by multiplying fawns:female X 100 X proportion productive (1.63 X 100 X 0.89 = 145).

[c] Data from adjacent NCRCA study area.

[d] Total does not include 1975 NCRCA data.

then compared to fawn:female ratios for full coverage aerial surveys during autumn, early winter, and spring, to determine survival. Another ratio determined for June each year was an estimate of what the annual maximum fawn:female ratio could have been (Table 5.2). This was obtained by using the highest observed fawn-at-heel ratio (1.76 fawns:female) and also assuming that all females except yearlings were pregnant.

During 1975-1986, an average of 14% (range 0-42%) of potential fawn production was lost prior to the time fawn-at-heel ratios were obtained in mid-June (Table 5.3). This loss of potential production represented 18% of the total

Table 5.2. Estimated maximum possible fawn:100 female ratios, estimated fawn:100 female ratios during mid-June, and observed fawn:100 female ratios during autumn, winter, and spring, 1975-1987.

Time Period	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
Potential[a]	157	165	148	158	125	132	137	139	130	162	171	158
mid-June[b]	145	141	125	148	125	126	126	123	113	100	99	148
late Sept.	72	62	80	107	120	88	79	72	76	43	31	77[c]
late Dec.	47	44	52	105	116	88	79(76)[d]	82(72)[d]	68(67)[d]	34(33)[d]	29	77
early April	14	39	31	85	104	78	55	72	17	6	21	73

[a] Potential fawn production assumes that all females 2 years old and older were pregnant and that the maximum observed fawn-at-heel ratio (1.76) was possible every year.

[b] See footnotes to Table 5.1 for method of estimation.

[c] Actual observed ratio was 67:100, but the December ratio was also used for September because the autumn flight was earlier than usual and, apparently, all females were not regularly accompanied by their fawns.

[d] Ratio in parenthesis necessary for September-December mortality calculations because adult females were harvested disproportionately more than fawns.

Table 5.3. Finite rates of fawn mortality expressed as percentages for various time periods, Missouri River Breaks, Montana, 1975-1987.

Time Period	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	Mean	CV
Potential-June	7.6	14.6	15.5	6.3	0.0	4.6	8.0	11.5	13.1	38.3	42.1	6.3	14.0	0.93
June-Sept.	50.3	56.0	36.0	27.7	4.0	30.2	37.3	51.0	32.7	57.0	68.7	48.0	41.6	0.41
Oct.-Dec.	34.7	29.0	35.0	1.9	3.3	0.0	3.8	0.0	11.8	20.9	6.5	0.0	12.2	1.13
Jan.-May	70.2	11.4	40.4	19.0	10.3	14.3	30.4	12.2	75.0	82.4	27.6	5.2	33.2	0.38
June-May	90.3	72.3	75.2	42.6	16.8	38.1	56.4	41.5	85.0	94.0	78.8	50.7	61.8	0.38
Potential-May	91.1	76.3	79.1	46.2	16.8	40.9	59.9	48.2	86.9	96.3	87.7	53.8	65.3	0.38

number of fawns lost annually. Recruitment of fawns to 1 year of age averaged 35% of maximum potential and ranged from 83% in 1979 to 4% in 1984. Generally, the loss of potential production prior to mid-June was low, but was exceptionally high during 1984 (38%) and 1985 (42%). Losses from the estimated maximum production to mid-June included non-breeding, non-pregnancy, less than maximum ovulation and fertilization rate, abortion, resorption, stillbirth, and immediate post-partum abandonment.

Of fawns surviving to mid-June, an average of 42% (range 4-69%, Table 5.3) died by late September. The lowest rate of mortality during summer was for the 1979 cohort; the highest for the 1985 cohort. The rate of fawn mortality during summer was less variable than during autumn and winter (Table 5.3). Mortality was exceptionally low during summer 1979, but exceeded 30% during all other summers except 1978 (28%). Of all fawns dying between mid-June and the following May, 65% died by the end of September.

Mortality rate of fawns during autumn averaged 12% (range 0-35%), was lower than during any other season (Table 5.3), was more variable (CV=113%) than during any other season, and was generally either very low or very high. Highest mortality was observed during 1975, 1976, 1977, and 1984. Overall, however, only 9% of the fawns that died during their first year of life died during autumn.

Over-winter mortality rates averaged 33% (range 5-82%) and accounted for 26% of all deaths of fawns. Although winter was longer than other periods, almost all mortality occurred by the end of March, so mortality rates were generally comparable among seasons. Mortality rates during winter were high during 1975-76, 1983-84, and 1984-85; moderate during 1977-78, 1981-82, and 1985-86; and lower during other years.

Total annual mortality for fawns that were alive in mid-June averaged 62% and ranged from 17 to 94%. Annual mortality was less than 50% during only 4 of 12 years. Despite annual mortality of fawns that usually exceeded 50%, population growth occurred in some of these years. With no hunting mortality, adult female numbers increased slightly from spring 1976 to spring 1978 despite annual fawn mortality of 72% for the 1976 cohort and 75% for the 1977 cohort. Adult female numbers increased substantially from 1978 to 1979, when annual fawn mortality was 43%. Despite annual fawn mortality of 56% and 42% and moderate hunting mortality of adult females, the number of adult females also increased somewhat from spring 1981 through spring 1983.

Seasonal estimates of fawn mortality were further refined by calculating instantaneous monthly rates of mortality for

radio-collared fawns during 1976-1986 (Fig. 5.2). Mortality rates were highest (r>0.10/month) during June, July, August, and February. Mortality was moderate during September, October, January, and March, and very light during November, December, April, and May.

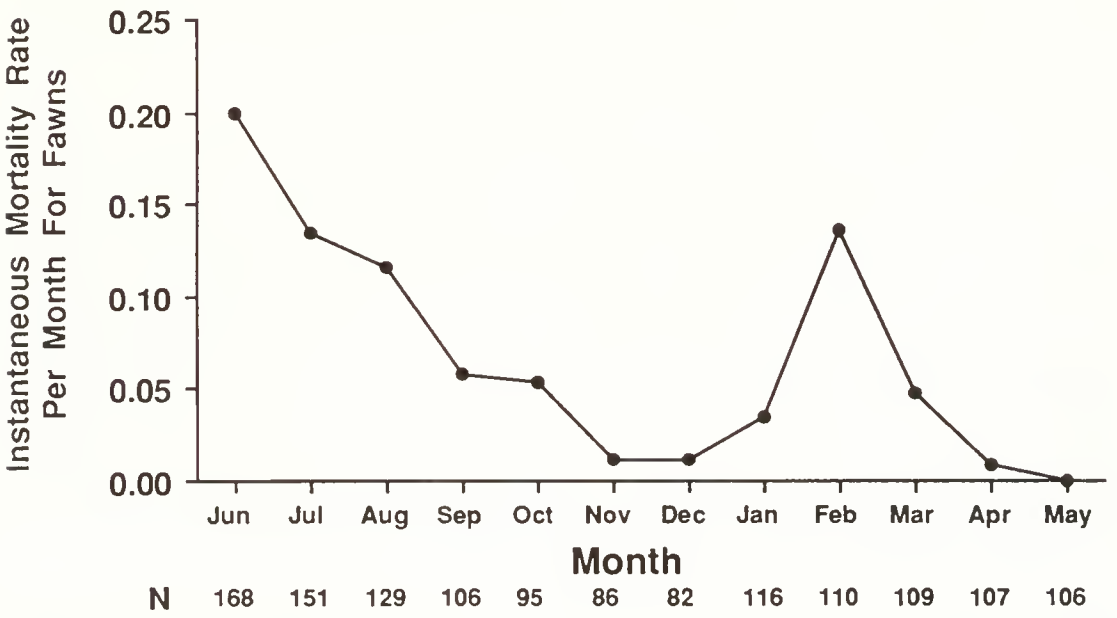


Figure 5.2. Instantaneous monthly mortality rate for radio-collared mule deer fawns, 1976-1986.

1960-1974

Early winter classifications were made during most years of this period (Table 4.2), but autumn (Table 4.1) and spring (Table 4.3) classifications were made during few years prior to 1975. Assuming average fawn production each year, annual first-year mortality rates were 43%, 69%, 62%, and 53% for the 1960-1963 cohorts. Annual mortality was 89% for the 1971 cohort and 77% for the 1972 cohort. Because spring classifications were not made during other years, annual mortality could not be calculated directly.

Observed fawn mortality rates were 12%, 24%, <1%, and 14% during autumn; and 4%, <1%, <1%, and 17% during winter for the 1960-1963 cohorts, respectively. Observed winter fawn mortality rate was approximately 77% for the 1971 cohort.

Mortality during other years was calculated from population estimates and/or average mortality rate for other years with similar weather patterns. Calculated fawn mortality rates for 1960-1974 were similar to those observed during 1975-1986. Autumn mortality was generally low, as during 1975-1986, but was somewhat higher during 1960-1963 because of higher harvests of antlerless deer. Autumn mortality was highest during the severe drought year of 1961. Winter mortality was generally low during both periods, except for occasional catastrophic mortality.

Age-specific Fawn Production and Recruitment

Fawn production and survival records were obtained for 114 marked females during June 1976-May 1984 (Hamlin and Mackie 1987). Twenty-seven provided information only on breeding success as fawns. The remaining 87 females included 34 (39%) known-aged deer captured as newborn fawns or as 1/2 or 1-1/2 year olds. Another 16 (18%) were aged by eruption-wear techniques (Robinette et al. 1957) at capture and later by dental cementum techniques at death. Thirty-seven females (43%) were aged only by eruption-wear. Data on fawn production and survival were not complete for all females during each period of the year, thus data presented here are a composite, by age class, over the 8 year period.

None of 41 female fawns sampled had bred (Fig. 5.3). Among older females, production increased steadily with age, reaching a peak for females breeding at 5-1/2-years and giving birth at 6 years. Production declined for females giving birth at 7 years and remained lower than for 3 to 6 year old females thereafter. Production for 7-year-old females was 12%, 16%, and 21% lower than for 4-, 5-, and 6-year-old females, respectively. Production was similar for 3- and 7-year-old females, but 7 year old and older females produced 22% more fawns than first year breeders.

Females of ages 4, 5, and 6 years had the highest recruitment rate of fawns to 6 months. Recruitment to 6 months declined substantially for 7-year-old females and increased somewhat thereafter, but never returned to rates sustained by 4-, 5-, and 6-year-old females.

Recruitment of fawns to 12 months was highest for females giving birth at 4 and 5 years and declined considerably after 5 years, generally remaining higher only than recruitment rates of first year breeders.

The highest rate of fawn loss during summer and autumn occurred among females giving birth at 3 and 7 years; the lowest was for 4- and 5-year-old females. The highest rates of over-winter fawn loss were for 2-, 6-, 8-, and 9-year-old

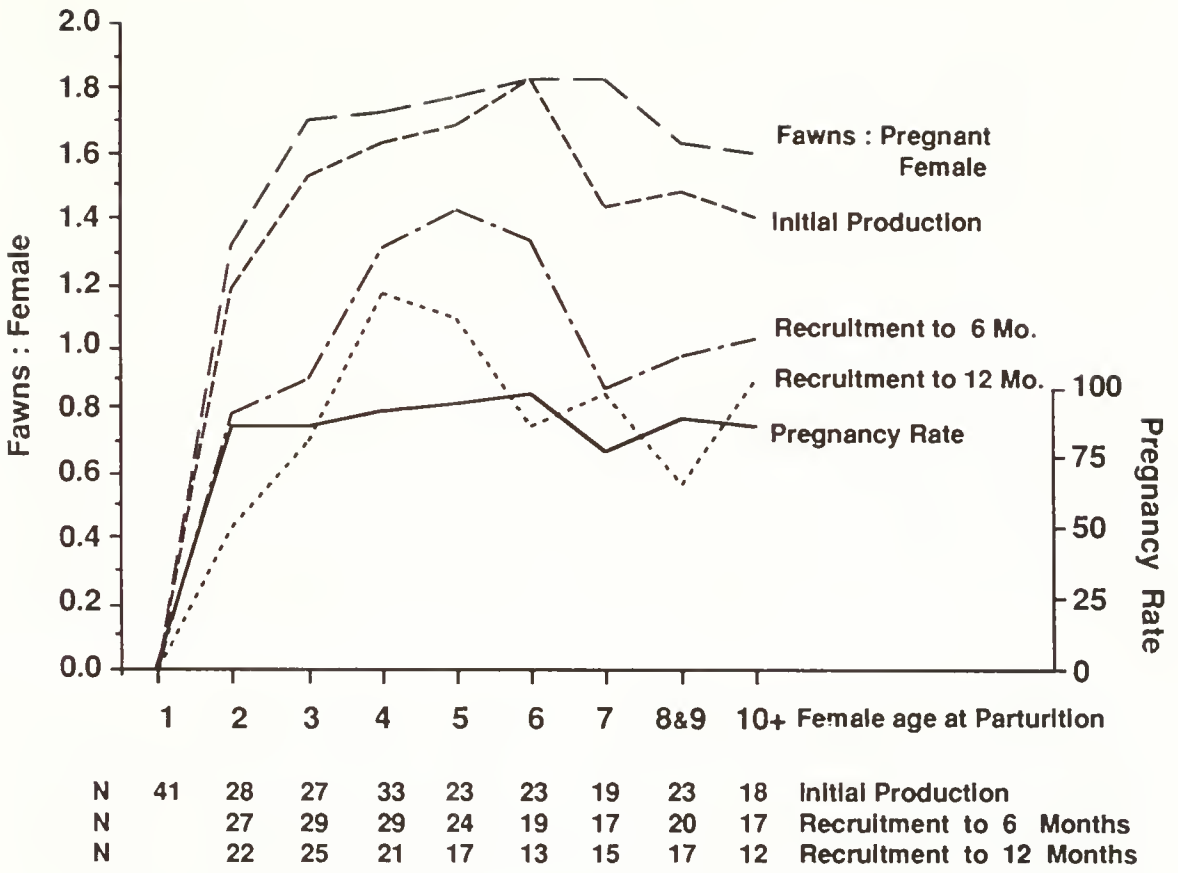


Figure 5.3. Age-specific production and recruitment of fawns by female mule deer in the Missouri River Breaks, Montana, 1976-1984.

females, and the lowest were for 4-, 7-, and 10+ year olds. The highest rates of fawn loss over the entire 12 month period occurred among 2-, 6-, 8-, and 9-year-old females.

Recruitment of fawns to 12 months was the first parameter to decline with age, decreasing slightly from 4- to 5-year-old females and substantially from 5- to 6-year-olds. Recruitment to 6 months declined slightly from age 5 to 6 and substantially from age 6 to 7. Most of this decline was related to a decline in pregnancy rate, because the number of fawns per pregnant female did not decline until between 7 and 8 years of age.

Speculations about the effects of previous reproductive status on age-specific recruitment rates were based on 87 pairs of years. We used recruitment to 6 months as the reproductive parameter because it indicated that the female had undergone full lactation stress. Sample size by age class ranged from 10 to 15 cases. Over all age classes, 55% of females recruited fawns to 6 months in successive years, 38% in alternate years, and 7% did not recruit fawns for 2 successive years. Females of age 4, 5, and 6 years were most likely to recruit fawns when they had also recruited fawns the previous year (71%). Eight and 9-year-old females were least likely to recruit fawns in successive years (27%). Females of ages 3, 8, and 9 years were most likely to recruit fawns in only 1 of 2 years (57%).

Trends in age-specific fawn production and recruitment (Fig. 5.3) were generally typical of mammals (Caughley 1977); climbing from puberty and forming a convex plateau. However, relative declines after middle age were more severe than typically seen. Data presented by Clutton-Brock et al. (1982) also indicated a similar abrupt decline in fecundity for middle-aged red deer hinds on the island of Rhum. Their data, however, indicated a subsequent recovery in fecundity that we did not observe.

Some additional data were collected on reproduction and recruitment by age class during 1984 and 1985, both years of drought and nutritional stress. Data for recruitment to late autumn for small samples of females observed during 1984 and 1985 (Table 5.4) indicated that all age classes of females produced and recruited fewer fawns than during 1976-1983. Very few fawns of the 1984 and 1985 cohorts were recruited to 1 year of age (6 fawns:100 females in 1984 and 21:100 in 1985). Females giving birth at 3 years and at 7 years and older, declined the least in fawn recruitment relative to the average for 1976-1983. First year breeders and females giving birth at 4, 5, and 6 years underwent the greatest decline in recruitment.

Nutritional stress appeared to have greatest influence on first time breeders, as commonly reported, but females normally producing the most fawns (4-, 5-, and 6-year-olds) also were greatly affected. Except for first year breeders, females giving birth at 3 years and 7 years of age and older had recruited fewer fawns per capita the prior year than other deer (Table 5.4). Thus, at least some members of those age classes were most likely to be in the best condition during 1984 and 1985 and consequently produced most of the recruited fawns. Four- to 6-year-old females, that usually recruited the highest number of fawns per capita, may have been in the poorest condition going into 1984 and 1985 because of cumulative reproductive stress, and thus experienced the

Table 5.4. Age-specific fawn recruitment to late autumn for female mule deer during 1984 and 1985, compared to the average for 1976-1983.

Female Age Class	1984 and 1985 Number of Females	1984 and 1985 Number of Fawns	1984 and 1985 Fawns Per Female	1976-1983 Fawns Per Female	1984 and 1985 as a Percentage of 1976-1983
1 -2[a]	8	1	0.13	0.81 (27)[b]	16
2 -3	11	5	0.45	0.93 (29)	48
3 -4	13	4	0.31	1.34 (29)	23
4 -5	12	4	0.33	1.46 (24)	23
5 -6	10	2	0.20	1.37 (19)	15
6 -7	5	2	0.40	0.88 (17)	45
7 -9	9	4	0.44	1.00 (20)	44
9 +	7	4	0.57	1.06 (17)	54
TOTAL	75	26	0.35	0.90 (182)	39

[a] Age at conception -- age at parturition.
[b] Female sample size.

greatest decline in recruitment of fawns. First year breeders experienced an equally great decline in recruitment, probably because more than for other age groups, nutritional demands of body growth competed with reproductive demands.

Based upon estimated age structure, 3-year-old and 7-year-old-and-older females produced 54% of fawns surviving through late autumn in 1984 and 1985. If recruitment had been equivalent to the average for 1976-1983, those age classes would have produced 32% of surviving fawns. However, the difference in survival by female age class had no measurable impact on the population because few fawns of the 1984 and 1985 cohorts survived to 1 year of age regardless of the age of their mother.

Population Effects of Age-Specific Recruitment

We hypothesized that age-specific variation in recruitment of fawns, in conjunction with changes in age structure of the female population, might explain declines in fawn survival on the area during the early-mid 1970s. However, analyses using several different models did not support that hypothesis. Numbers of fawns produced and fawn:100 female ratios generated by the models are presented in Table 5.5. Calculations were based on female age structure (Fig. 4.9) and the recruitment by age class observed during

Table 5.5. Effect of observed age-specific fawn recruitment compared to stable recruitment by age class on numbers and ratios of fawns recruited as female age structure varied, Missouri River Breaks, Montana, 1968-1986.

Year	Number of Females	Number of 2+ Females	Number of Fawns Recruited			Fawns: 100 Females			Fawns:100 2+ Females		
			A1[a]	B1[b]	C1[c]	A2	B2	C2	A3	B3	C3
1968	535	375	294	311	285	55	58	67	78	83	96
1969	565	425	301	353	400	53	63	83	71	83	111
1970	680	480	357	399	340	53	59	59	74	83	84
1971	745	575	434	477	70	58	64	17	75	83	21
1972	460	425	347	356	115	75	77	34	82	83	37
1973	390	335	299	274	125	77	70	42	89	83	49
1974	355	295	264	242	75	74	68	27	89	83	33
1975	310	275	228	229	35	74	74	13	83	83	14
1976	290	275	230	227	100	79	78	39	84	83	41
1977	305	255	228	212	95	75	70	33	89	83	39
1978	335	290	231	241	250	69	72	83	80	83	96
1979	415	300	228	247	410	55	60	103	76	83	142
1980	550	400	287	332	410	52	60	77	72	83	106
1981	680	530	381	439	300	56	65	55	72	83	70
1982	700	550	424	456	415	61	65	72	77	83	91
1983	790	580	484	480	120	61	61	17	83	83	23
1984	760	700	555	579	40	73	76	6	79	83	7
1985	675	655	561	544	140	83	81	21	86	83	22
1986	730	660	601	547	470	82	75	70	91	83	77
Mean	541	441	354	366	221	67	68	48	81	83	61
SD	177	147	123	122	151	11	7	28	6		39
CV	33%	33%	35%	34%	68%	17%	11%	59%	8%		64%

[a] A = number or ratio of fawns recruited, using 1976-1983 age-specific variation in recruitment data (Fig. 5.2) and female age structure (Fig. 4.9).

[b] B = number or ratio of fawns recruited, assuming that each age class 2+ produced the 1976-1983 average (0.83) fawns per capita.

[c] C = observed number or ratio of fawns recruited.

1976-1983. Alternative estimates of fawn numbers and ratios were generated by assuming that all females older than yearlings recruited fawns at the same average rate.

Numbers

Given the estimated female age structure each year from 1968 through 1986, there was little difference in the average number of fawns recruited whether recruitment varied by age for females (Column A1, Table 5.5) or whether recruitment rate was the same for all 2+ females (Column B1, Table 5.5). Fawn production did not vary significantly more than numbers of females producing those fawns in either case. Number of females producing fawns was more important to total fawn production than age-specific differences in fawn recruitment among females. The greatest difference in fawn recruitment for any individual year was during 1969, when variation in recruitment by age class produced about 15% fewer fawns than would have been produced by equal recruitment by all age classes (Table 5.5).

Potential differences in fawn recruitment between the 2 models are shown in Figure 5.4. When the population was expanding and had relatively more females in younger age classes, fawn recruitment would have been somewhat depressed by the age-specific variation in recruitment observed during 1976-83. The reverse was true in declining populations with relatively more older animals. In neither case, however, would general population trend be greatly affected. The observed number of fawns recruited (Column C1, Table 5.5) varied considerably more than any variation owing to age-specific differences in recruitment. Age-specific differences in fawn recruitment, operating as an intrinsic mechanism of population control, probably contributed a relatively minor amount of the observed variation in fawn recruitment.

Ratios

We observed little variation in average fawn:female ratios between the model assuming age-specific differences in recruitment (Column A2, Table 5.5) and the model assuming equal recruitment across all age classes (Column B2, Table 5.5). The same was true for fawn:2+ female ratios (Columns A3 and B3, Table 5.5). Observed fawn:female and fawn:2+ female ratios (Columns C2 and C3, Table 5.5) varied considerably more than ratios assuming constant recruitment.

Given the female age structures estimated for each year 1968-1986, and assuming that annual fawn recruitment was stable for the population but varied among age classes as observed for 1976-1983, fawn:female ratios could have varied from 52 to 83:100 with a mean of 67:100 and a coefficient of

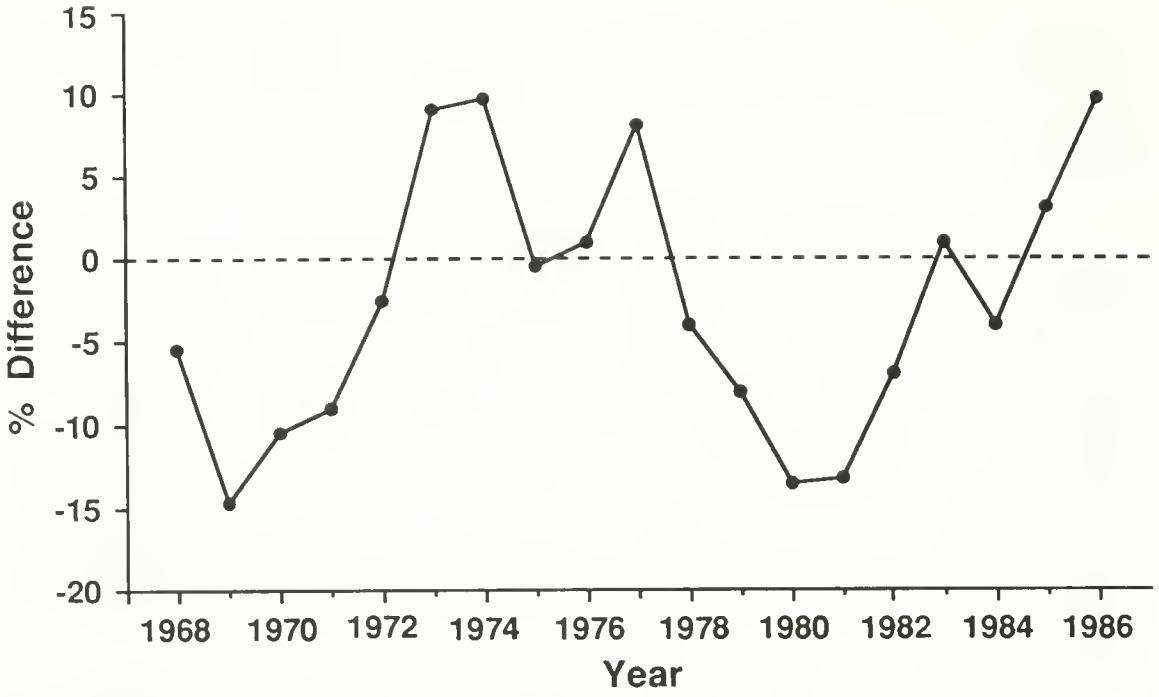


Figure 5.4. Percent difference in number of fawns recruited when the age-specific variation observed was compared to the number recruited if all age classes of females had recruited the same average number of fawns, 1968-1986. The line at zero % difference represents no age-specific difference in fawn recruitment rates.

variation of 16.5% (Table 5.5). Lower ratios prevailed in growing populations that included large numbers of non-productive yearlings and lower producing 2-year-old females. Higher ratios prevailed when relatively few younger animals and relatively more 3-5 year old females were present. The projected degree of variation due to age-specific differences in recruitment and female age structure (Columns A2, B2, and A3, Table 5.5) was relatively minor compared to observed variation in ratios (Columns C2 and C3, Table 5.5). The observed low recruitment during 1972-1977, for example, cannot be explained by age-specific differences in recruitment and female age structure. Age-specific differences in recruitment combined with female age structure should have led to higher than average fawn:female ratios during that period (Table 5.5).

Although the ratios in columns A or B and C are not directly comparable, the degree of variation about the mean (CV) was informative. Data from modeled and observed numbers and ratios (Table 5.5), indicated that a maximum of 30% of the observed variation in fawn:female ratios was related to age-

specific differences in recruitment and female age structure; 70% or more was related to factors influencing fawn survival across all female age classes. The contribution by non-age-related factors must have been even greater during 1972-1977 when age-related factors should have resulted in above-average ratios.

Although age-specific differences in recruitment are interesting, valuable for comparison with deer in other environments, have implications for individual survival, and help explain condition cycles, they probably did not explain major population changes on our study area. Some age classes may be affected to a greater degree than others by conditions influencing fawn recruitment (1984-85, Table 5.4), but major changes in fawn recruitment apparently were the result of factors affecting all age classes rather than individual age classes.

Fawn Mortality Related to Litter Size and Sex

Proportions of fawns of single (38.7%) and twin (31.4%) litters that died during summer, 1976-1986, were not significantly different (X^2=0.62, P=0.45, 1 df, n=167 fawns). Mortality rate of male fawns (n=82) was not different for litter size (X^2=0.03, P=0.88, 1 df), nor was a difference apparent for female fawns (X^2=1.06, P=0.33, 1 df, n=85). Overall, male and female fawns died at similar rates during summer (X^2=0.24, P=0.65, 1 df). However, during years of poor fawn survival (1976, 1977, and 1983-1985), 62% of 37 female fawns died and only 40% of 38 male fawns died (X^2=3.01, P=0.09, 1 df). During other years, no difference was apparent in mortality of female (17%) and male (25%) fawns (X^2=0.53, P=0.48, 1 df). Although the relationship was statistically marginal for this small sample, the possibility of lower survival for female fawns during years of higher fawn mortality may warrant further investigation. An additional substantiation of this relationship was the fact that 9 of 10 fawns captured during December 1983 (a cohort of poor survival) were males.

Proximate Causes of Fawn Mortality

Determination of causes of fawn mortality was based on annual samples of 10-19 radio-collared newborn fawns during 1976-1986. Although these sample sizes were small, they indicated the same trend in mortality rates during summer as indicated by changes-in-ratios (Fig. 5.5). Generally, few fawns retained radio-collars during autumn and winter, and they were used only to determine cause of death during that time.

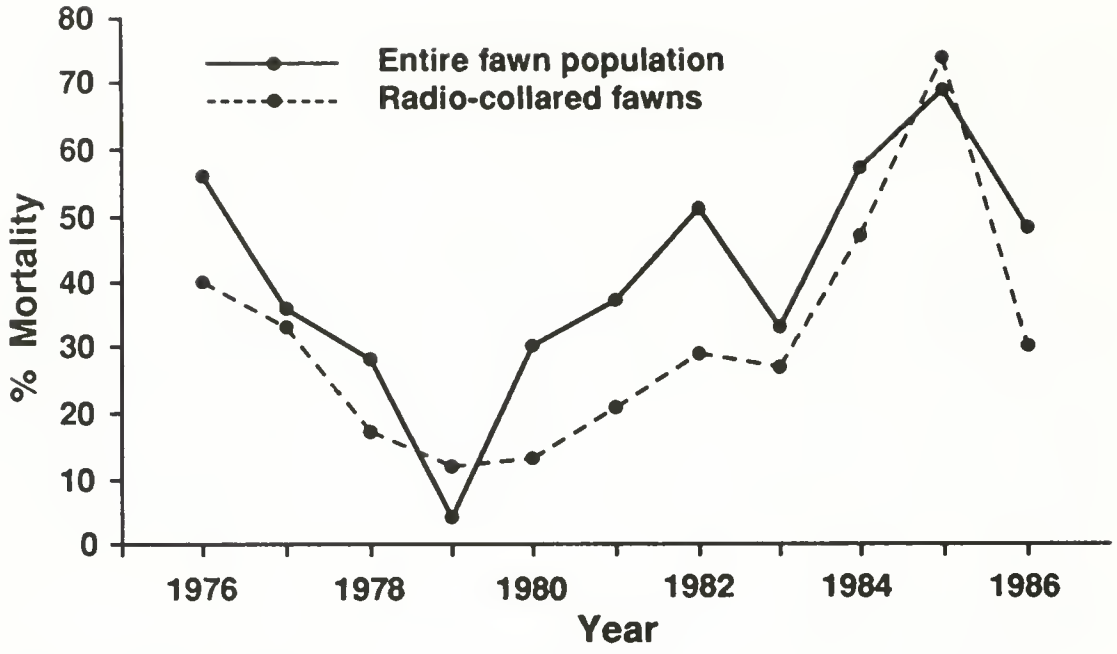


Figure 5.5. A comparison of finite summer mortality rates between small samples of radio-collared mule deer fawns and the entire fawn population, as determined by change-in-ratio calculations, 1976-1986.

Coyote predation was the major cause of death for fawns during summer. Eighty-nine percent of all deaths (48 of 54) of radio-collared fawns during summers 1976-1986 resulted from known or probable coyote predation (Table 5.6). Additionally, 1 died as a result of accidental suffocation, and 2 (all during 1984) as a result of non-capture related abandonment. Cause of death for 3 fawns was unknown.

Cause of death was established for 4 unmarked fawns during summer. Three were victims of coyote predation and 1 died as the result of a disease resulting in diarrhea. Only during 1984, when non-capture related abandonment was observed, did any fawn appear to be in obviously poor condition at or after the time of capture. Four abandonments believed related to capture and handling were recorded, one each during 1978, 1979, 1980, and 1983. Those fawns were not included in mortality calculations.

Coyote predation and hunter harvest were the primary causes of fawn mortality during autumn. Four (57%) of 7 deaths of radio-collared fawns for which cause was established were the result of coyote predation. Two were shot (1 legally and 1 illegally), and 1 died as the result of an infection from a puncture wound between the hooves. One unmarked fawn

Table 5.6. Summer mortality and causes for radio-collared mule deer fawns 1976-1986.

Year	Number of Fawns Monitored	Number Died	% Mort.	Number of Definite or Probable Coyote Killed	Unknown	Other	% Coyote Killed
1976[a]	10	4	40	4			100
1977[a]	18	6	33	5		1	83
1978[b]	12	2	17	1	1		50
1979[b]	17	2	12	2			100
1980[b]	15	2	13	2			100
1981	19	4	21	4			100
1982	17	5	29	4	1		80
1983	11	3	27	3			100
1984	19	9	47	6	1	2	67
1985	19	14	74	14			100
1986	10	3	30	3			100
TOTAL	167	54	32	48	3	3	89

[a] Data from Dood (1978) and personal communication.
[b] Data from Riley (1982) and personal communication.

was known to have died from internal injuries of unknown origin.

Antlerless deer (including fawns) could not be legally harvested during 1976-1980. Estimated hunter harvest of fawns in 1981 and 1982 was about 7-8% of the prehunt fawn population and about 2-3% in 1983 and 1984. Too few fawns were checked in the hunter harvest during 1985 and 1986 to make valid estimates. Data from field checks of hunters during 1960-1962 indicated that approximately 8%, 20%, and 13% of prehunt fawn populations were harvested during those years. A special late season antlerless hunt during 1961 resulted in a greater than average harvest of both fawns and adult females. Even during autumn, mortality from other causes usually accounted for more fawns than did hunter harvest.

Hunters selected against fawns as compared to adult females. During 1960-1962 and 1981-1984 when relatively large samples of antlerless deer were checked, comparison of the proportions of fawns and adult females in harvests and the pre-season populations indicated average harvest rate for fawns was 59% (range, 43-73%) of that for adult females.

Apparently, the stigma of shooting fawns went beyond the actual harvest. During 1981-1984, only 18% (range, 14-22%) of the observed proportion of fawns checked was reported on post-hunt questionnaires.

The proximate cause for 21 (95%) of 22 deaths of radio-collared fawns during winter was coyote predation. The remaining fawn died as the direct result of malnutrition. All unmarked fawns found dead during winter died as the result of coyote predation (see Chapter 4).

Ultimate Causes of Fawn Mortality

Although the proximate cause of death for 73 (88%) of the 83 radio-collared fawns that died was coyote predation, we also addressed other factors as potentially contributory or predisposing fawns to predation. Other studies in the western United States also determined that predation was the major proximal cause of deer fawn mortality (Cook et al. 1971, Beasom 1974, Steigers and Flinders 1980, Trainer et al. 1981, and Stout 1982). The ultimate causes of mortality and their population impacts have remained subjects of debate (Hamlin et al. 1984).

Beasom (1974) and Stout (1982) indicated that predator control increased fawn survival. Circumstantial evidence on our study area during the late 1940s and early 1950s also indicated that predator control increased fawn survival. Others (Knowlton 1976, Robinette et al. 1977 and Salwasser et al. 1978) suggested that vegetation production, through its impact on nutritional status and fawn hiding cover, may be an ultimate factor in fawn mortality. Smith and LeCount (1979) indicated that mule deer fawn survival in Arizona was related to forb yield. Hamlin et al. (1984) also found a possible relationship between forb yield and summer fawn mortality, but suggested that the real relationship may have been between alternate prey levels for coyotes and fawn mortality. They suggested that populations of microtine rodents varied with vegetation production.

It has become axiomatic among many population biologists and most wildlife managers that, ultimately, food shortage and nutritional considerations are paramount in regulating juvenile survival, especially in non-territorial species. The concept that predators kill only the young, the old, the weak, and the sick has been presented directly, or has its roots in information presented to the public by these same scientists. Implicit in this idea was the fact that food shortage often caused these animals to be in poor physical condition, predisposing them to predation.

The formal idea that populations are ultimately controlled by food probably began with the writings of Malthus, first published in 1798 (Davis 1950). Davis (1950), from the perspective of game management, stated: "Our modern game managers have ample evidence that inadequate food supplies render a species susceptible to various mortality factors." Malthus noted that an epidemic is followed by healthfulness because the weak are killed, and there is more room and food for the survivors. This concept has been applied by wildlife biologists to the effect of predators on their prey populations.

Although qualifications are often given, the idea that food can be, and ultimately is, the factor limiting ungulate populations is basic to most comprehensive publications relating to wildlife management (Leopold 1933, Lack 1954, Dasmann 1971, Caughley 1976b and 1977, and McCullough 1979). Theories of density-dependence and compensatory mortality and reproduction rely on the implicit assumption that food and/or space are limiting the population and that mortality varies directly with forage-nutrition levels. Caughley (1977) states: "Should the (population) decline be a consequence of reduced food supply or poor habitat the diagnostic feature is a rise in juvenile mortality, usually coupled with a decline in juvenile fecundity."

More recently, Peek (1980) summarized current management philosophy as follows:

> "Very often resource management is based on an unrecognized underlying hypothesis. In the case of native ungulates, the hypothesis that a weather-forage complex regulates populations is implicit in much habitat and population manipulation. The alternative -- that predation controls populations -- is widely accepted also."

Data collected during this study enabled us to examine the relationships among fawn mortality, predation, forage production and deer condition, winter severity, and deer density.

Fawn Mortality In Relation To Forage Production

Multiple regression analysis indicated that fawn survival to December was related to the same factors which were highly predictive of forage production: precipitation from July through April prior to the growing season, and mean temperature during May (see Chapter 3). Thus, we substituted July-April precipitation and mean May temperature for forage production estimates, to compute regressions relating fawn survival to forage production annually from 1960 to 1986.

Fawn:female ratio during December was the dependent variable used to represent relative fawn survival.

In addition to estimates of forage production, other independent variables evaluated included: mean temperature for the winter prior to birth, the number of adults in the population at parturition, the number of adults one year prior to parturition, and the average number of adults for the 2 periods. We included mean winter temperature as an index to winter severity because of the possibility that severe winters might reduce condition of the female, thereby affecting subsequent fawn survival. Numbers of adult deer were included to cover possible density effects and lag effects of density.

We did not expect a regression including all years to result in a significant relationship, and it did not (R^2 = 0.195, F = 1.33, P = 0.29). Although fawn survival generally followed forage conditions in most years, some notable exceptions (1974-1975) were apparent. Low survival of fawns during the early to mid-1970s, despite apparently good forage conditions, was one factor leading to initiation of the intensive phase of this study. Because of this, we used a "step-up" multiple regression technique. The regression was initiated with those years which most appeared to fit a forage-fawn survival relationship. Additional years were added to the regression, retained if they significantly fit the regression and dropped if they did not. About 80% of the variation in fawn:100 female ratios in December was explained by the independent variables of the regression for 21 of 27 years, 1960-1986 (R^2 = 0.805, F = 37.25, P < 0.00001). Forage production variables of July-April precipitation and mean May temperature were the only variables that were significant in predicting fawn survival to December [$\hat{Y}$ (fawns:100 females) = 437.5 - 7.39 (May temp.) + 3.15 (July-Apr. ppt.)]. Winter severity and deer density did not add significantly to the overall regression over any combination of years.

We also compared fawn survival directly with the forb and shrub production observed and estimated by regression for the measured plots. A simple linear regression of fawn survival against forage production for the same 21 years included in the multiple regression indicated a significant relationship (r=0.873, P < 0.01). When an index for available forage per capita (kg forage/ha/number of adult deer 1 June) was regressed against fawn survival, the relationship was significant (r=0.627, P < 0.01), but less than that for non-density adjusted forage production.

Data on relative fawn survival through spring (fawn:adult ratios) were available for 15 years. Fawn survival through spring was significantly (R^2=0.659, F=11.57, P=0.002) related to the same variables (July-April precipitation and mean May

temperature) as for fawn survival to December, but less of the variation was explained. Again, neither variables relating to deer density or winter severity added significantly to the regression. We expected current winter severity to play a greater role in determining fawn survival through spring, but the effect of winter severity was apparently not consistently linear. Instead, it acted catastrophically during some years and inconsistently during others.

An underlying relationship appeared to exist during most years between fawn survival to December and variables for precipitation and temperature prior to birth. Because there was no relationship with deer density or lag effects of density, it is doubtful that the relationship we observed was related to forage quantity. Fawn survival should not have been directly related to forage quantity only, but to relative forage quantity as influenced by deer density (forage per capita).

We believe the relationship of July-April precipitation and mean May temperature with fawn survival was one of forage quality to fawn survival, rather than forage quantity to fawn survival. Forage quality was not measured directly; only general observations were recorded. Based on the literature (Mackie et al. 1979, Short 1981, and Wallmo and Regelin 1981), we assumed that forage nutritional quality was highest in growing plants and declined at and after plant maturation.

Blaisdell (1958) found that phenological development was correlated with temperature and precipitation during the growing season. He stated, "Early in the spring, phasic development of plants is controlled chiefly by temperature, but later in the season temperature becomes less important and development is hastened by a shortage and retarded by an abundance of moisture." Wielgolaski (1974) and White (1979) also indicated that temperature was very important in determining plant phenological development. When spring temperatures were high, plants grew and matured faster, reducing the time that they provided quality forage, and reducing their total yield. The same temperature and precipitation variables correlated with increased yield also were correlated with delayed plant maturation and a longer period of quality forage (Blaisdall 1958). That relationship agreed with our observations that forage generally remained succulent longer during years that also had the highest forage yield.

Although both precipitation and temperature were important, most variation in forb yield was explained by mean temperature during May. Most variation in shrub yield was explained by precipitation during the previous July-April period (Chapter 3). When fawn survival was regressed against

these variables, mean temperature during May explained 67% of the variation in fawn survival and July-April precipitation an additional 14%. Because forage per capita was not closely related to fawn survival, the relationship of mean May temperature to fawn survival probably was a reflection of the relationship between spring temperature and phenological development of forbs. High survival of fawns was related to cool spring temperatures, which resulted in slower plant development and a longer period of quality forage.

We examined residuals of the regression of July-April precipitation and mean May temperature on fawn survival to December to determine why 6 of 27 years did not fit the regression. The plot of residuals (Fig. 5.6) includes residuals for years which did not fit the regression (1965, 1969, 1974, 1975, 1980, and 1984). Fawn survival was significantly below expectations, based on forage factors, during both 1965 and 1984. Both years followed winters during which mortality was high and included adults, thus surviving females may have remained in poor condition through parturition and lost their fawns. Forage during those years was used to replace body fat reserves and muscle tissue rather than to rear fawns.

Similar winter mortality occurred during 1971-72. Although fawn survival was also lower than expected in 1972 (Fig. 5.6), it was not significantly lower. However, more adult females died that winter than in any other and thus did not survive to be recorded as barren females the next year. Moreover, a higher than usual percentage of the survivors that year may have been females that had not weaned a fawn the previous year and were in good enough condition to rear a fawn in 1972.

Fawn survival during both 1969 and 1980 was significantly above levels expected based on forage conditions. Both years followed 2 years of above-average forage conditions and were the third years of population increases. It is probable that fat reserves were built up over the 2 previous years and fawn survival was achieved on fat reserves of the females in addition to current forage.

During 1974 and 1975 (Fig. 5.6), fawn survival was significantly below that expected based on forage conditions. Those years followed 3 others (1971-1973) during which fawn survival was below expectations, although not significantly so. Both casual observations and the results of our regressions indicated that poor fawn survival during the early- to mid-1970s, and especially 1974 and 1975, should not have been the result of poor forage conditions. Additionally,

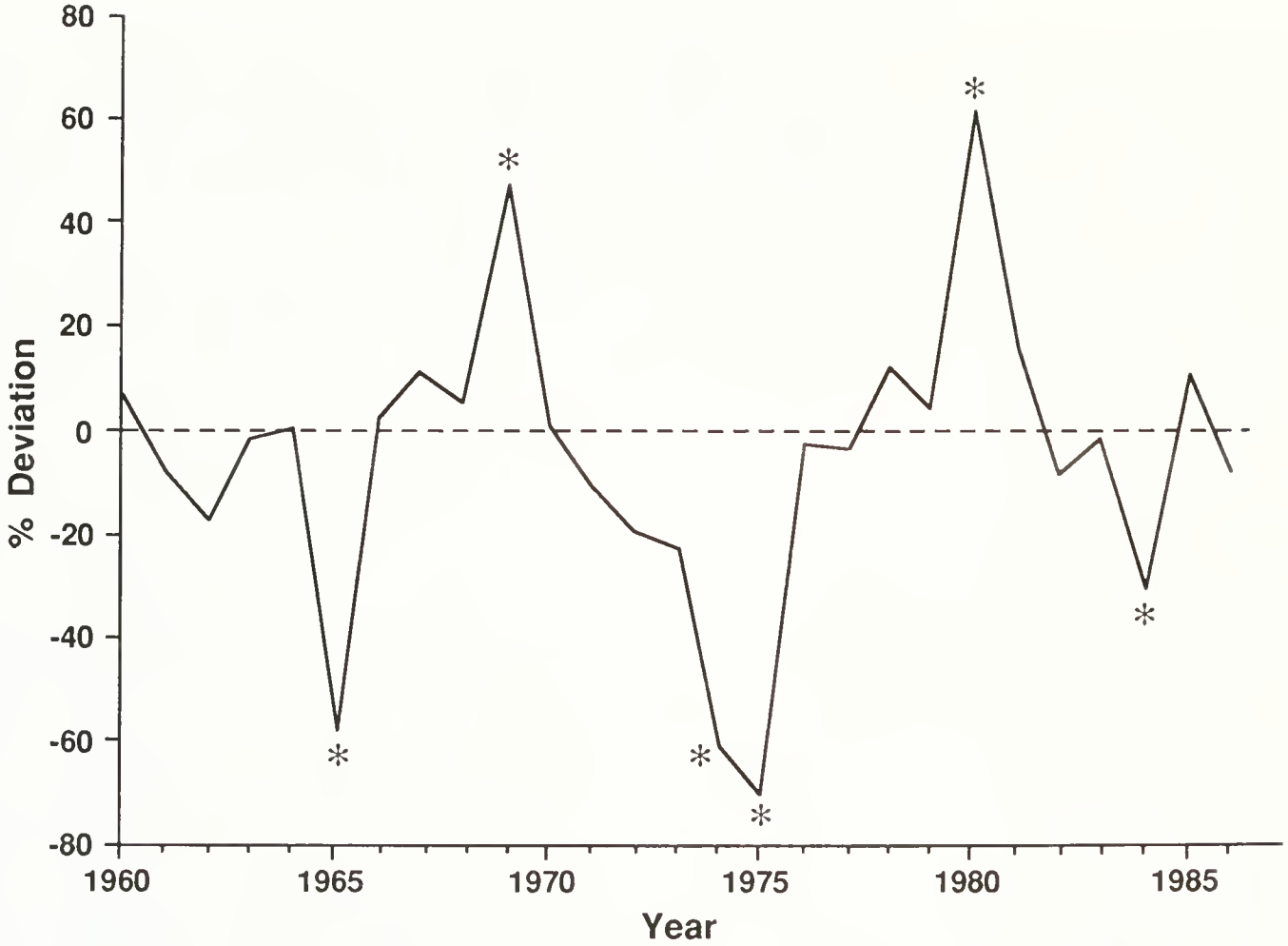


Figure 5.6. Residuals of the multiple regression of fawns:100 females in December against precipitation during July-April and mean May temperature plotted as % deviation of the observed ratio from the predicted ratio. Years marked with an asterisk do not fit the regression.

available information indicated that deer were in average or better condition during those years.

We conclude that in most years, fawn survival is directly related to forage quality as determined by the length of time plants remain green and succulent, providing quality forage for lactation. Four of the 6 years excepted may be explained by cycles of fat storage and depletion. If fat reserves are high, females may be able to produce and nurse fawns successfully, despite poor quality current forage. On the other hand, a female coming out of winter in extremely poor condition, with a loss of muscle tissue as well as fat, may lose her fawn *in utero* and/or not have recovered enough to successfully rear a fawn, despite good forage conditions during summer.

The assumption inherent in regressions of fawn survival against estimates of forage production is that improved forage conditions result in improved physical condition of deer and, in turn, higher fawn production and survival. Studies of captive deer document that improved nutrition results in improved deer condition and improved fawn production and survival (Verme 1962, 1965, 1969; and Robinette et al. 1973). French et al. (1956), Robinette et al. (1973), and Rasmussen (1985) further suggested that antler characteristics of yearling males were sensitive to nutritional conditions.

Because we collected data on antler characteristics of yearling males relatively consistently, we were able to regress those data against annual forage production estimates. All antler characteristics and measurements of yearling male mule deer were positively related to forb production (Table 5.7), which should indicate that deer condition improved with increased forage production and quality. As with previous regressions of fawn survival on forage production, antler size (if it was related to forage quantity) should be better-related to forage per capita than just relative annual forage production. Antler measurements regressed against an index of forage per capita also indicated significant relationships, but rather than improving the relationship, the inclusion of a deer density factor weakened the relationship (Table 5.7). Because of that, we believe the relationship of antler size with forage production estimates was not with forage quantity, but with coincident forage quality.

Trends in fawn survival and antler characteristics of yearling males coincided during most years (Fig. 5.7). This relationship was especially apparent during 1960-1964 and 1977-1986, underscoring the general relationship between fawn survival, deer condition, and forage conditions. Even the exceptions tended to verify the expectation that antler size and deer condition were related to forage conditions. Fawn

Table 5.7. Correlation coefficients for regressions of antler characteristics of yearling male mule deer against forb production and per capita forb production, 1976-1986, Missouri River Breaks, Montana.

Dependent Variables	Independent Variables					
	Forb Production (kg/ha)			Per Capita Forb Production (kg/ha/deer)		
	r	P	n	r	P	n
Number of antler points per side.	0.793	<0.01	11	0.703	<0.05	11
Percentage antlers 2x2 points per side or more.	0.789	<0.01	11	0.751	<0.01	11
Beam diameter (mm)	0.799	<0.01	10	0.603	0.06	10
Product of beam diameter and percentage antlers 2x2 points per side or greater.	0.825	<0.01	10	0.792	<0.01	10

survival during 1965 was much below expectation based on current forage conditions. Both number of antler points per side and % 2X2 point antlers of yearling males, however, increased in 1965 over that of 1964 (Fig. 5.7), as expected, based on forage conditions. That information verified our projections that forage conditions were good during summer 1965, and that fawn survival was probably poor because of lag effects in female condition following the preceding severe winter.

Forage conditions were apparently sufficient to result in average or better antler size of yearling males during 1973-1977, when fawn survival was lower than average (Fig. 5.7). Although forage conditions were excellent during 1975, the 2 measurements of antler size displayed in Figure 5.7 declined. However, another measure of antler size (beam diameter) was near the highest recorded (Table 4.7). Antler size that year, regardless of the measure used, was at least near average, and certainly greater than in 1961, 1984, and 1985, when deer were in extremely poor condition and antlers were extremely small.

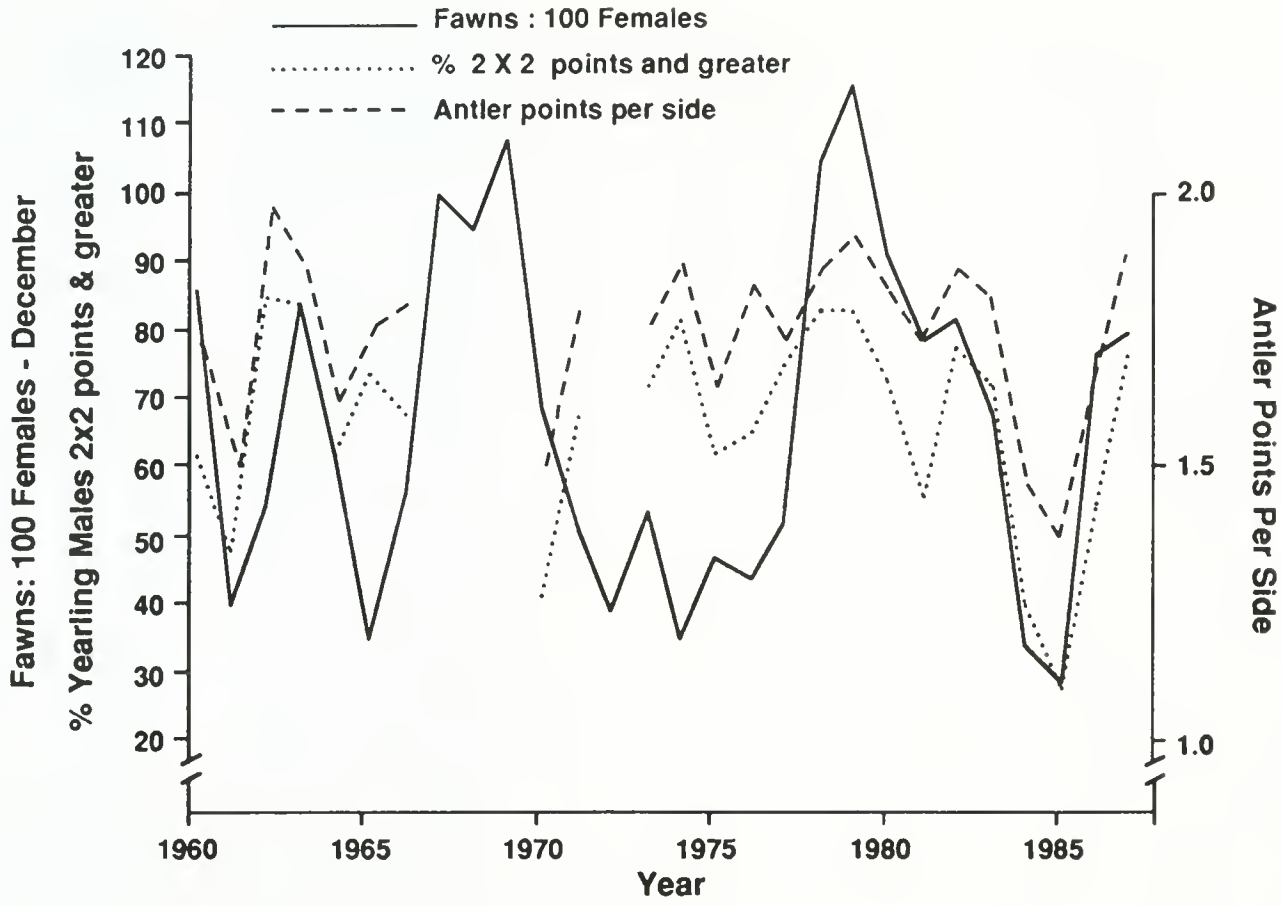


Figure 5.7. Trend in fawn:100 female ratio in December, 1960-1987, compared to the trend in number of antler points per side for yearling males and the trend in % yearling males with 2x2 point or greater antlers.

The combination of information available on fawn survival, forage production, and antler size (deer condition) indicated that poor fawn survival during 1973-1975 did not result from poor forage conditions or poor physical condition of the deer population.

Effect of Coyote and Alternate Prey Populations on Fawn Mortality

Fawn survival rates during 1976-1987 were influenced by coyote predation which was influenced by alternate prey population level. Especially for microtine rodents, population level probably was related to vegetation production.

Coyote populations on the study area were estimated by siren answer surveys and den area surveys (Pyrah 1984, Hamlin et al. 1984). Siren-answer surveys were also conducted in the Yellow Water Triangle, about 65 km south of our study area, during 1972-1978 (Pyrah 1987). Although density estimates were lower on prairie habitats of the Yellow Water Triangle than our study area, coyote populations followed the same trend during 1976-1978. Density estimates for 1976-1978 were almost identical on the Yellow Water Triangle (Pyrah 1987) and prairie areas immediately adjacent to our deer study area (Pyrah 1984). This relationship was used to estimate siren-answer values and coyote density for our study area during 1972-1975 (Fig. 5.8).

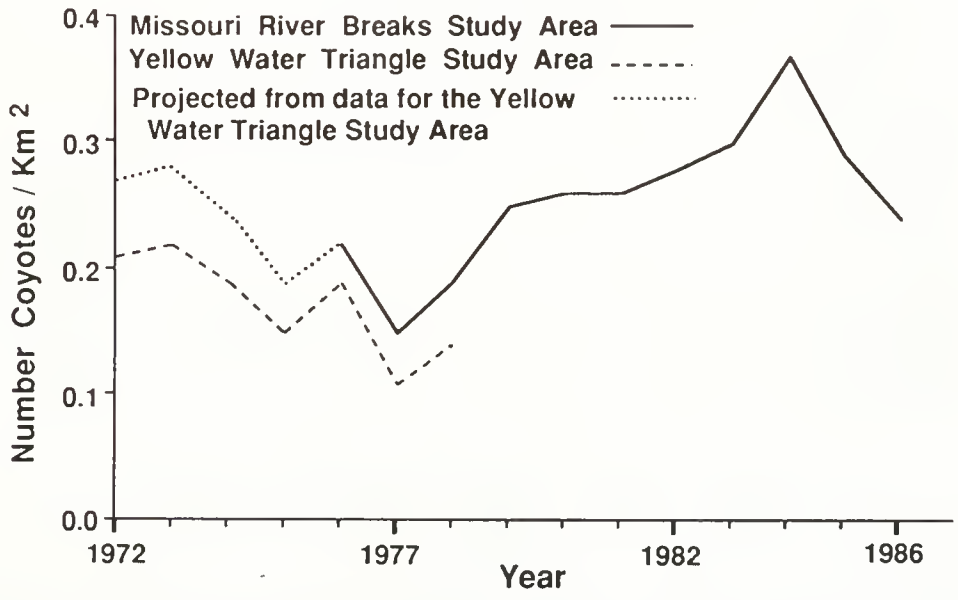


Figure 5.8. Coyote density, as determined by the siren-answer survey, for the Missouri River Breaks and Yellow Water Traingle study areas.

Numbers of coyotes responding to the siren during summer declined from 1972-1973 to a low in 1977 (Fig. 5.8). Estimated coyote numbers increased from 1977 to 1984 and then declined through 1986. Notably, and contrary to general public perception, coyote populations on both areas declined following the 1972 ban on the use of Compound 1080 for predator control.

Data on numbers of coyotes and the minimum number of litters on the study area during summer was provided by a combination of siren-answer and den area surveys (Pyrah 1984). Estimates for 1984-1986 may be low relative to prior years because den area searches were less intensive. Thus, numbers may not have declined to the degree indicated in Figure 5.9. It is possible peak numbers were actually reached during 1984, as indicated by siren-answers, and declined thereafter.

Total numbers of coyotes on the area during 1977-1985 (Fig. 5.9) varied by 1.6 times from low to high, a difference of 52 coyotes. That difference was mostly the result of variation in pup production and survival. The number of adults varied by 1.5 times from low to high, or 17 adults. Because pups comprise about one-half to two-thirds of summer coyote populations, it was not surprising that the minimum number of litters each year varied in a similar manner as total coyotes.

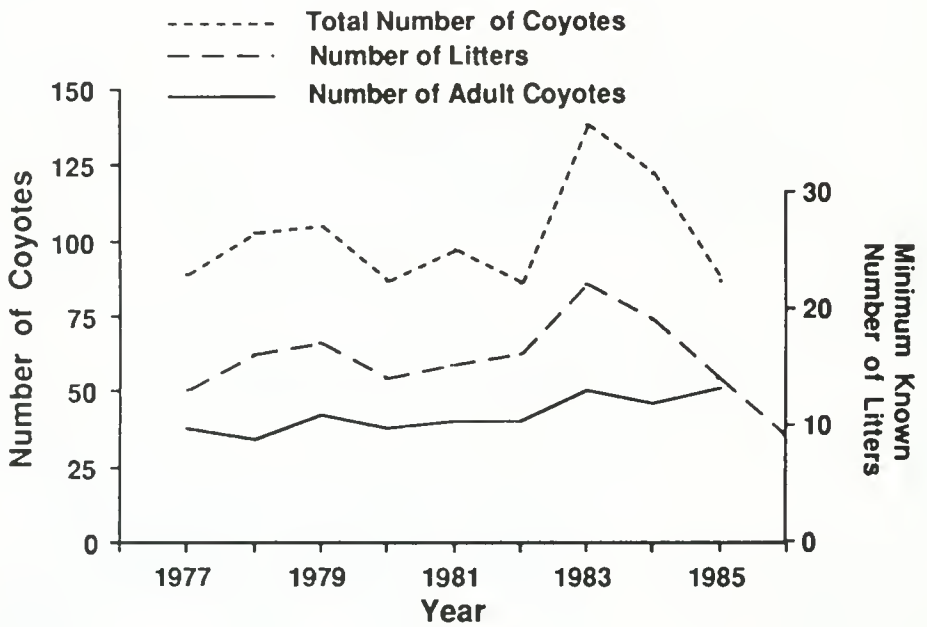


Figure 5.9. Number of coyotes and minimum number of coyote litters estimated for the Missouri River Breaks study area, 1977-1986, using a combination of siren-answer and den area surveys.

Populations of deer mice (*Peromyscus maniculatus*) increased irregularly from 1976 to 1983, declined abruptly in 1984, and slowly increased through 1986 (Figure 5.10). Microtine rodent (*Lemmiscus curtatus* and *Microtus* spp.) populations experienced 3 irruptions during 1976-1987. Populations were at peak levels from summer 1978 through autumn 1979 and from summer 1982 through autumn 1983. Another irruption started during summer 1986. No trapping was conducted during 1987, but field observations indicated that the irruption that started in 1986 continued through autumn 1987 and was at least as great as previous highs.

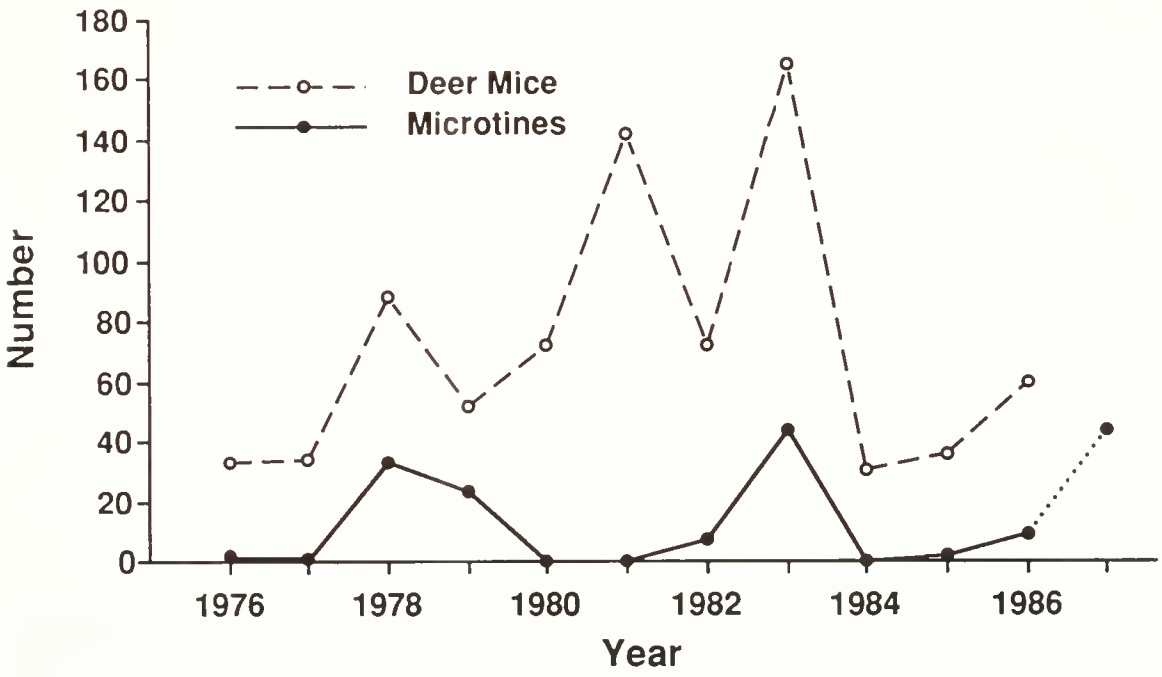


Figure 5.10. Number of individual deer mice and microtines captured on a live-trap grid on the Missouri River Breaks study area during summers 1976-1986. Dotted line for microtines in 1987 indicates estimated numbers.

White-tailed jackrabbit (*Lepus townsendii*) populations increased from 1976 through 1983, declined sharply by 1984 and remained low through 1986 (Figure 5.11). Numbers of cottontail rabbits (*Sylvilagus nuttallii*) observed during the surveys (Fig. 5.11) probably did not represent cottontail populations accurately because the routes were designed primarily for jackrabbits and included little good cottontail habitat. Notes from aerial radio relocation flights for deer

indicated that more cottontails were observed during winter 1982-83 than at any other time.

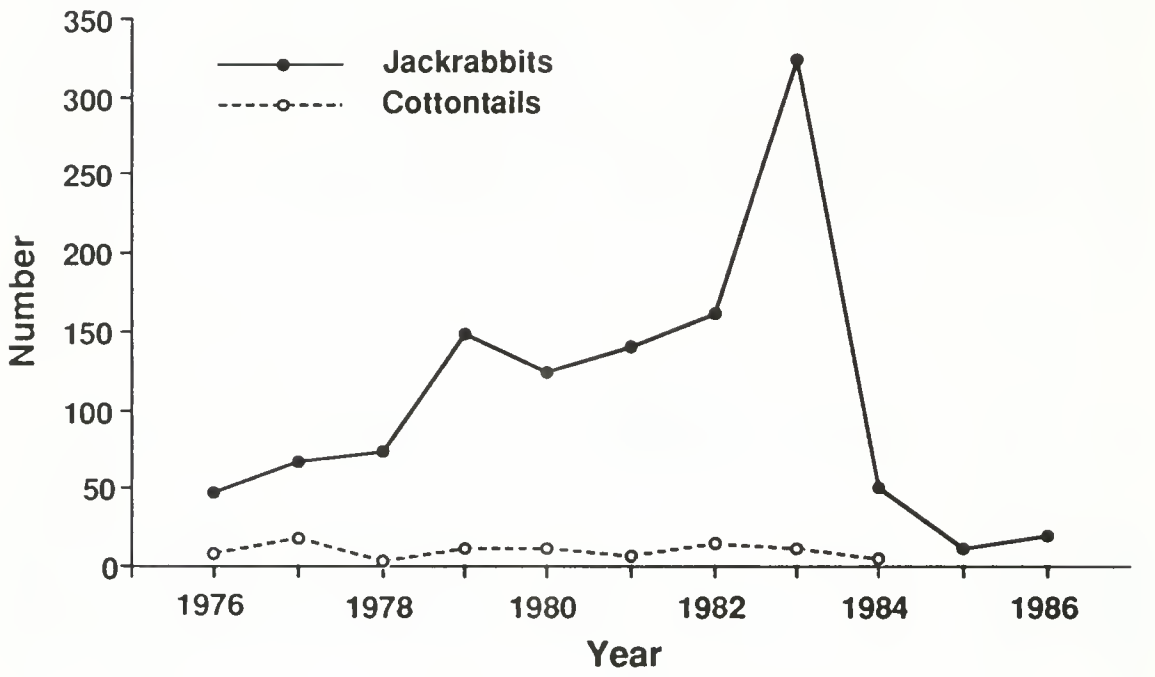


Figure 5.11. Number of jackrabbits and cottontail rabbits observed on a headlight survey route on the Missouri River Breaks study area during summers 1976-1986.

Coyote population levels may have been related to availability of rodents and rabbits on the area although not in a direct linear manner. Correlations between the siren-answer index one year and prey populations the previous year were significant, indicating that coyote populations increased the year following increases in prey populations. Correlation coefficients were 0.76 ($P = 0.01$) for coyote populations and jackrabbit numbers, 0.70 ($P = 0.03$) for deer mice, and 0.78 ($P = 0.01$) for an index combining jackrabbits, deer mice, and microtines. The combined index was based on coyote food habits (Hamlin et al. 1984); microtines were twice as important as deer mice, and all mice were twice as important as jackrabbits. The correlation coefficients were reduced by data for 1985 and 1986 because coyote populations did not decline as fast as prey populations. The relationship between minimum number of coyote litters and the siren-answer index to the alternate prey index is illustrated in Figure 5.12. Minimum number of litters may have responded to microtine populations more than other prey.

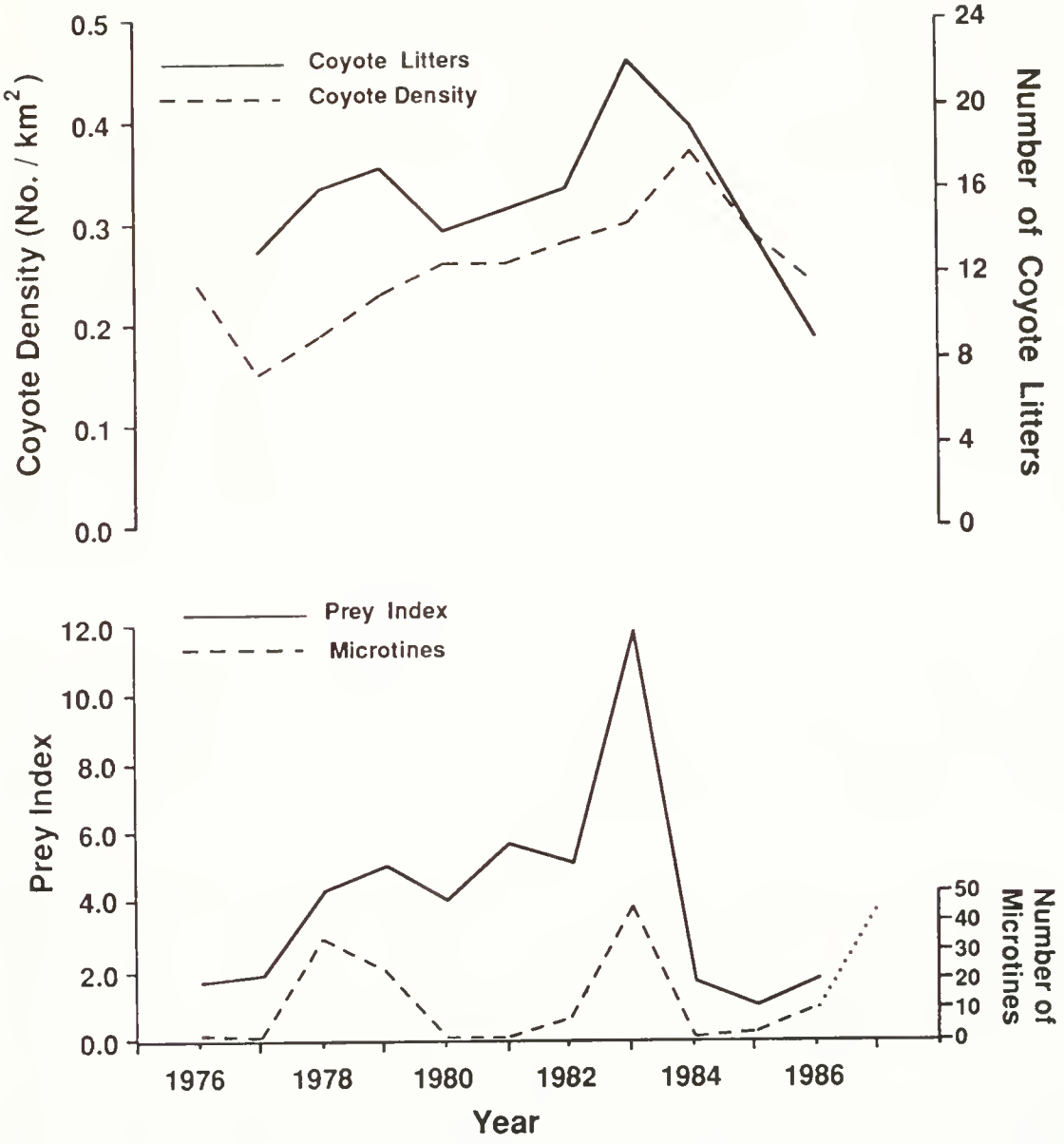


Figure 5.12. Relationships among the siren-answer index, total coyote numbers, the minimum number of litters, an index to alternate prey numbers, and microtine numbers.

Annual and seasonal fawn mortality rates (Table 5.5) were equally high during periods of low (1975-1977) and high (1983-1985) coyote populations (Fig. 5.8). Fawn mortality rates were not linearly related to coyote population level, as determined by the siren answer survey for annual or seasonal periods (all $r \leq 0.33$, $P > 0.05$). The small variation in the number of adult coyotes among years also made it unlikely that fawn mortality should vary with numbers of coyotes.

Although there was a tendency for fawn mortality to be lower when alternate prey populations were highest (Fig. 5.13), the relationship was not statistically significant. Fawn survival to autumn and winter was highest during microtine irruptions and lowest during the periods between microtine irruptions (Fig. 5.13). Use of average numbers of microtines during summer as an index may have obscured the relationship. Trapping in mid-summer and early autumn and general observations during 1978 indicated that microtine populations did not reach high levels until late summer, after almost all mortality of fawns that summer had occurred (Hamlin et al. 1984). Although more microtines than usual were present during 1982, highest numbers occurred from autumn 1982 through early summer 1983. Thus, most mortality of the 1983 cohort occurred after microtine populations had declined. Similarly, white-tailed jackrabbit populations peaked during summer 1983 and had "crashed" by November.

Population levels of microtine rodents were probably influenced by vegetation production. All 3 irruptions were concurrent with much greater than average production of grasses and forbs. A certain vegetation cover threshold may need to be met (Birney et al. 1976) before microtine population growth can take place.

Alternate prey populations, especially microtine rodents, influenced the degree of predation by coyotes on mule deer fawns. Annual fawn survival was lowest for the 1976, 1977, 1983, 1984, and 1985 cohorts (Fig. 5.13). All prey populations were at lows during those years, except 1983 when survival to early winter was relatively good for the 1983 fawn cohort, but overwinter survival was poor. Severe declines in both microtine rodent and jackrabbit populations had begun by autumn 1983. Consequently, much of the mortality of the 1983 fawn cohort occurred after alternate prey populations had declined.

Fawn survival increased substantially for the 1978 and 1979 cohorts, over that for 1976 and 1977 cohorts and coincided with both excellent forage conditions and a microtine rodent irruption. Populations of other alternate prey species were relatively low during 1978 and 1979.

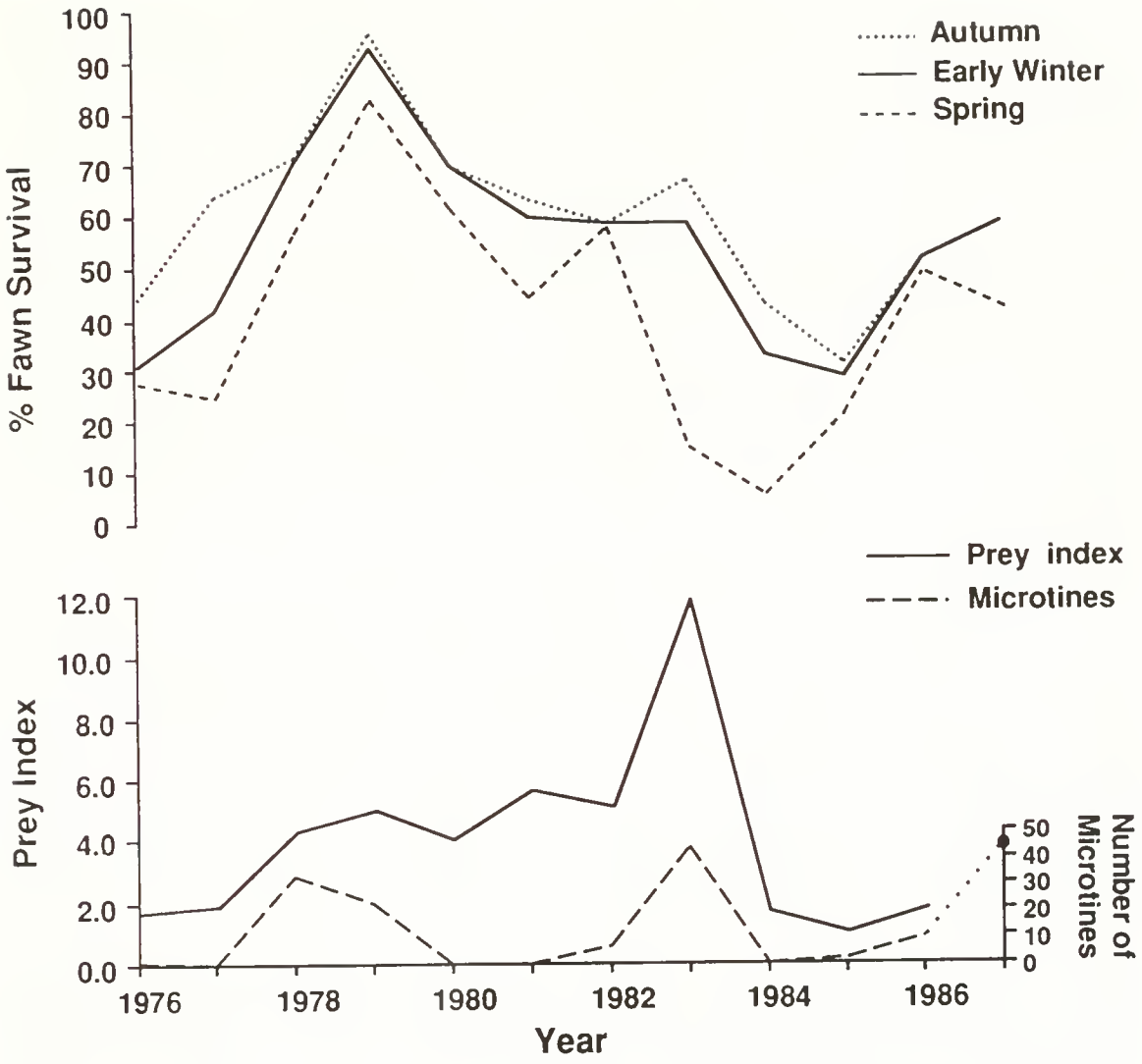


Figure 5.13. Relationships among fawn survival to autumn, early winter, and spring; an index to alternate prey numbers; and microtine numbers.

Although microtine populations had reached lows in 1980 and 1981, fawn survival did not decline to the degree of previous and subsequent declines (Fig. 5.13). Increasing numbers of deer mice and jackrabbits during 1980 and 1981 (Figs. 5.10 and 5.11) may have helped lessen the degree of decline in fawn survival during those years, though fawn mortality was relatively high during the severe winter of 1981-82.

Survival of fawns was not greater than average during summer 1982, but little mortality occurred after microtine populations began to increase during late summer. Fawn survival was high during summer 1983 but declined substantially after microtine and jackrabbit populations "crashed" in late autumn.

Drought conditions prevailed from late summer 1983 through late summer 1985. Both fawn survival and alternate prey populations were low during that period.

Survival increased substantially for the 1986 and 1987 fawn cohorts, coinciding with improved forage conditions initiated by heavy rains and an autumn "green-up" of vegetation during 1985. This was followed by an irruption and subsequently high microtine population from summer 1986 through autumn 1987.

Fawn Mortality in Relation to Winter Severity

Mortality of fawns during winter varied greatly among years (Table 5.5). Multiple regressions did not indicate a linear relationship between winter severity one year and survival of the subsequent fawn cohort. Winter severity and fawn mortality during the same winter were positively related ($r = 0.44$, $P < 0.05$, $N = 27$), but the relationship had many exceptions. When 5 years that deviated most were omitted from the regression, the relationship between winter severity and fawn mortality strengthened ($r = 0.655$, $P < 0.01$, $n = 22$).

Although winter fawn mortality might generally increase with winter severity (Fig. 5.14), prediction of fawn mortality based on winter severity alone could result in erroneous conclusions. Fawn mortality during the 2 most severe winters on record, 1977-78 and 1978-79, was about half that of 5 other winters, including 1975-76 and 1983-84, which were about 20% below the mean for winter severity. Winter severity was only slightly above the mean during 1984-85, but fawn mortality was the highest recorded. For most years when winter severity was near or below the mean (11.2), fawn mortality appeared to vary randomly between 4 and 30%. The winter severity index varied from below average (9.2) to very high (26.1) during winters when catastrophic mortality occurred.

Prior forage conditions helped explain some anomalies in the in the relationship between fawn mortality during winter and winter severity. Fawn mortality was high during winter 1964-65 despite only slightly more than average numbers of deer. However, forage quantity and quality were below average (Fig. 3.9) during summer 1964 and, although forage conditions were above average during summer 1963, they also were below

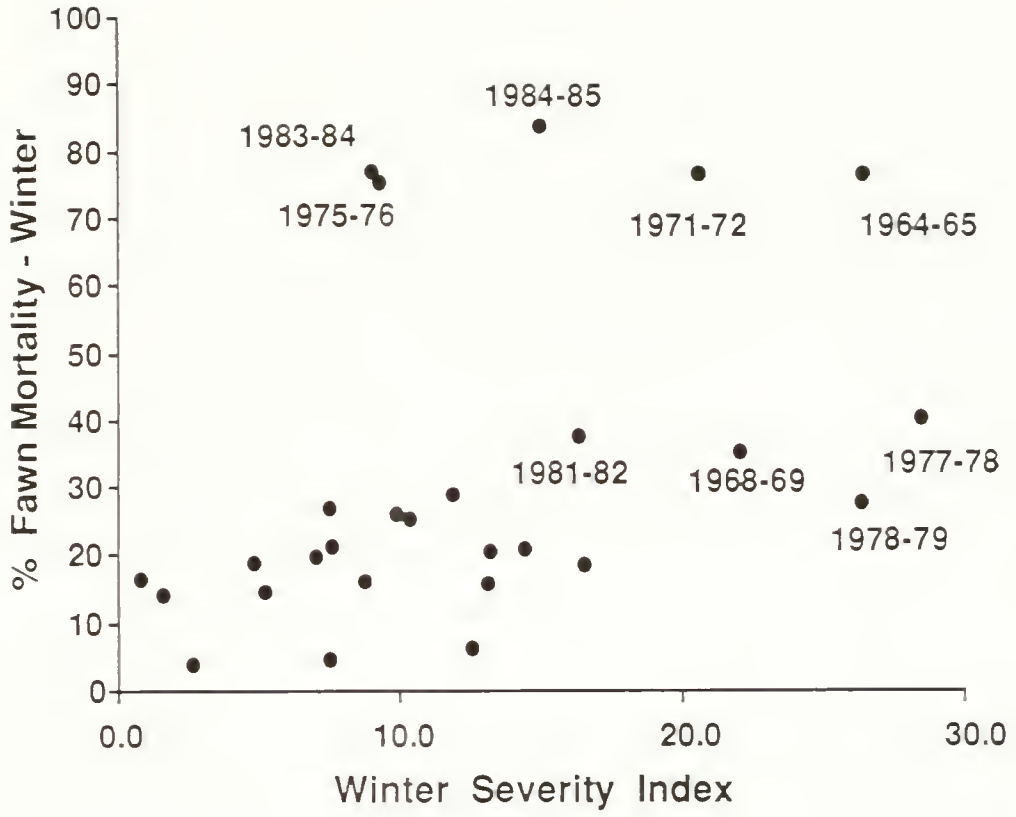


Figure 5.14. A plot of mule deer fawn mortality during winter against a winter severity index.

average during both 1961 and 1962. Thus, high fawn mortality during winter 1964-65 occurred when forage conditions had been poor for 3 of the 4 prior summers and deer were probably in relatively poor condition entering winter.

The winter of 1968-69 was very severe; the severity index was higher during only 3 other winters. Number of deer entering winter was at the long-term average and fawn mortality was moderately high, though not catastrophic. Forage conditions had been above average for 3 of the 4 prior summers (Fig. 3.9), and accumulated fat reserves probably enabled the deer population to get through winter without catastrophic mortality.

Winter severity during 1971-72 was similar to 1968-69; however, the number of deer in the population entering winter was above average. Catastrophic mortality of fawns and substantial mortality of adults occurred. Forage conditions were below average during each of the 3 previous summers (Fig. 3.9) and fawn production and survival had been high during the late 1960s suggesting both general body condition and fat reserves of deer were probably low at the onset of winter.

The winter severity index was the highest on record during 1977-78 and 1978-79, yet fawn mortality was moderate (Fig. 5.14). Although forage conditions were below average during early summer 1977, a late summer "green-up" enabled deer to feed on high-quality forage for about 3 months prior to the onset of winter. Deer numbers were low and deer were in good condition entering winter. Forage conditions were excellent during summer 1978, deer numbers were low, and deer continued to build body condition and fat reserves and were in good condition at the onset of winter 1978-79. Although moderate fawn mortality occurred during winters 1977-78 and 1978-79, it was much less than was expected considering mortality that occurred during winters of equal or lesser severity (Fig. 5.14).

Snow depth, which seldom exceeds 30 cm here, was greater than 75 cm more than 2 months during 1977-78 and exceeded 60 cm for more than 2 months during 1978-79. Persistent winds caused much drifting of snow and many shallow drainages were filled. Thus, snow depth precluded use by deer of most of the southern portion of the area. Even in areas where deer occurred, much of their normal food was inaccessible. Significant use of ponderosa pine needles by deer was detected only during those winters. Deer could only have survived by utilizing well-developed fat reserves.

Winter 1983-84 was slightly below average in severity and winter 1984-85 was only slightly above average in severity, but fawn mortality was catastrophic during both winters; many adult females also died during 1983-84. Numbers of deer were above average at winter's onset during each of the 2 years. Also, forage conditions were below average for 3 of 4 summers preceding winter 1983-84, and for 4 of the 5 summers prior to winter 1984-85. Fawn production and survival was high starting in 1978, and continued relatively high through early 1983, which probably required mobilization of body reserves during 1982 and 1983. Because of dry conditions during late summer and autumn 1983, deer probably entered winter in poor condition, with very low fat reserves.

The effect of winter severity on deer mortality appeared to be influenced by prior forage conditions. Numbers of deer

or density did not necessarily influence forage conditions, deer condition, or mortality.

Fawn Production and Survival in Relation to Density

Although one school of thought suggests that predators can control ungulate populations (Gasaway et al. 1983), the most widely accepted hypothesis is that a weather-forage complex regulates ungulate populations. This operates in a density-dependent manner through feedback mechanisms affecting fawn production and survival (Lack 1954, Caughley 1979, and Peek 1980). The latter holds that as density increases, increased demand for forage by ungulates ultimately has a detrimental effect on forage plants; declining forage quantity and quality subsequently lead to declining ungulate density. Implicit in this relationship are constant feedback and fluctuations in plant and animal components through which rates of increase in both are determined by ungulate density, assuming that everything else is equal. Because this system operates through a feedback loop, the density-dependent effect is often delayed. The existence of this density-dependent system is most apparent through changes in juvenile production and mortality because juvenile survival is most sensitive to reduced food supply (Caughley 1977).

Theories involving density-dependence have usually assumed a more or less determinate carrying capacity (K). More recently, Caughley (1977) recognized that density-dependence is most likely to operate in its purest form in areas where environmental fluctuation is minimal. Species or populations living in widely fluctuating environments such as the Missouri River Breaks would be least likely to exhibit density-dependent phenomena, but to date few species or populations have been placed in this category (Caughley 1977).

The data we collected over 28 years enabled us to examine the question of density-dependent regulation for this central Montana population and determine the extent to which variation in fawn production and survival was density-dependent.

Initial production of fawns (fawn-at-heel ratios) during 1976-1987 was not significantly ($P > 0.05$) density-dependent (Fig. 5.15), nor did the assumption of a 1-year lag effect result in statistical significance. Little change in fawn-at-heel ratio occurred until adult female numbers were more than 750, when a sharp decline took place. However, the decline which took place in 1984 and 1985 (Fig.5.15) may not have been related to density and the same decline could occur at any population level if an equally severe drought occured. Conception and pregnancy are probably less costly in terms of energy and resources than lactation, so initial production was

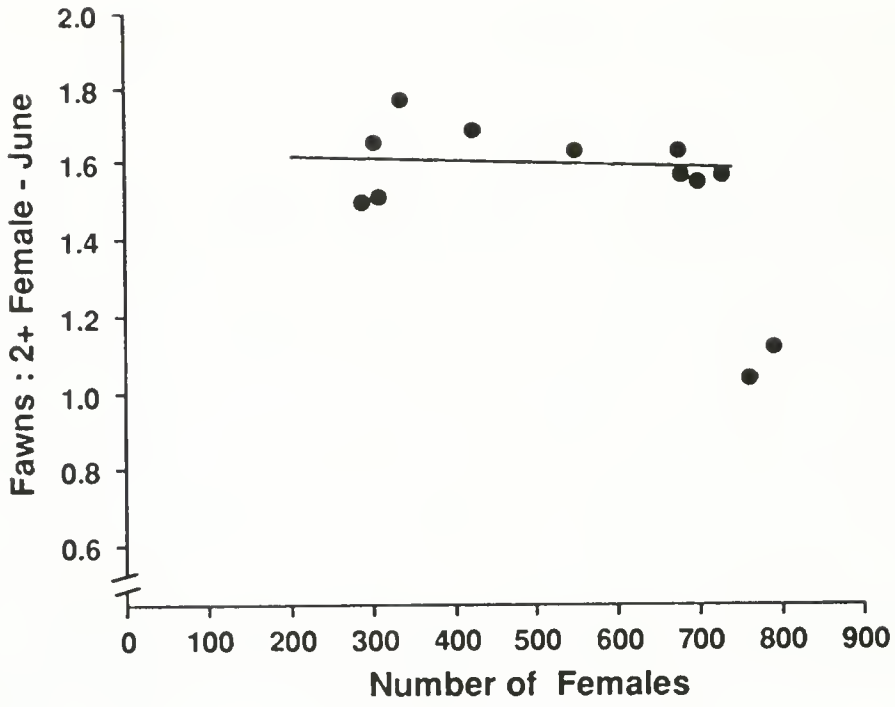


Figure 5.15. Fawn-at-heel ratio during June plotted against number of adult females in the population during June.

expected to be less sensitive than survival to density. Thus, it is likely that initial production remains relatively stable except during very extreme conditions, such as the drought from late summer 1983 through 1985.

Per capita fawn recruitment rate to December for breeding-age females was not statistically significantly related to the number of breeding-age females ($r = -0.171$, $P > 0.05$, Fig. 5.16). Although highest per capita recruitment rates occurred at low to moderate densities, low recruitment rates occurred at all densities. Recruitment deviated most from density-dependent expectations during 1973-1977 (furthest lower left points, Fig. 5.16). When data from those years were excluded, a more general decline in recruitment with density was apparent. However, fawn recruitment was substantially below expectations during some years of moderate density and above expectations during some years of high density. Overall, recruitment during almost half of all years deviated considerably from levels expected for the most extremely direct density-dependent linear relationship (Fig. 5.16).

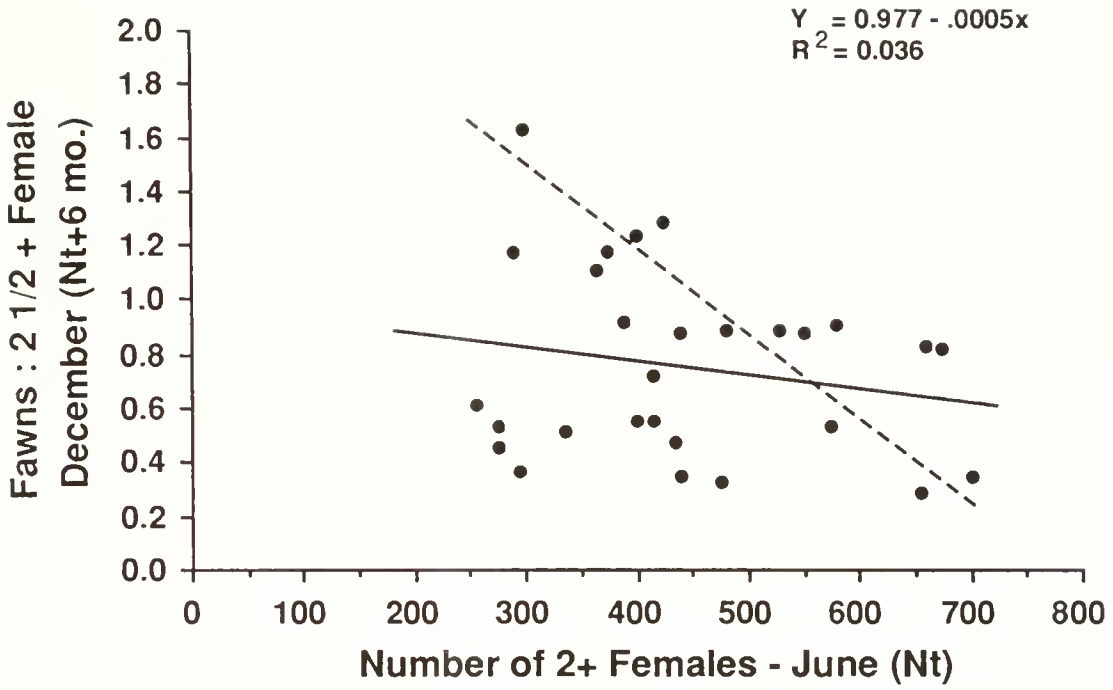


Figure 5.16. Fawns:mature female during December plotted against number of mature females in the population at birth pulse. Solid line is the actual regression line, the dashed line represents theoretical complete linear density-dependent fawn survival.

Per capita recruitment of fawns to 1 year of age for breeding-age females was also not significantly ($r = -0.052$, $P > 0.05$) related to the number of adult deer present the previous spring (Fig. 5.17). A slightly more negative, but still non-significant ($r = -0.246$, $P > 0.05$), relationship occurred when per capita recruitment to 1 year of age was regressed against numbers of breeding-age females, rather than total adults.

Although there may possibly be an underlying decline in recruitment with increasing density, it has little management application. From the standpoint of hunting management, the manager clearly can not depend upon high compensatory recruitment rates at low densities (Figs. 5.16, 5.17).

Fawn mortality rates were also plotted against deer density for those who prefer data expressed in that manner (Figs. 5.18 and 5.19). No significant linear relationship ($P > 0.05$) existed between fawn mortality rate to 1 year of age

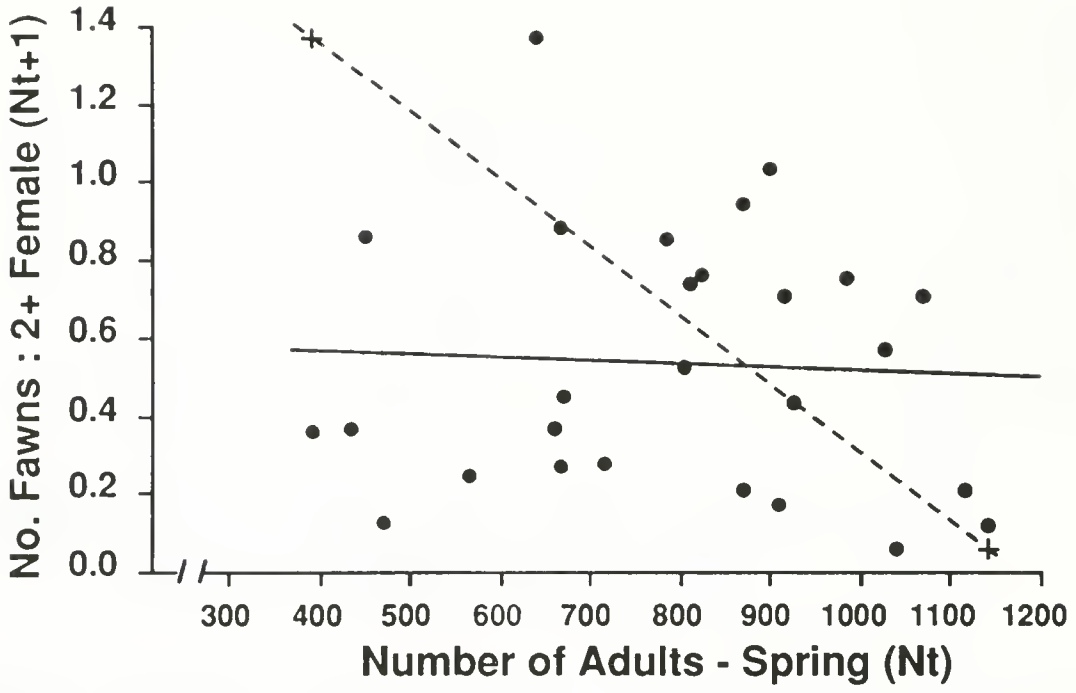


Figure 5.17. Number of fawns per adult female in spring plotted against the number of adults in the population at birth pulse when the cohort was born. Solid line is the actual regression line, the dashed line represents theoretical complete linear density-dependent fawn survival.

and deer density at birth pulse ($r = -0.06$, $n = 27$, Fig. 5.18) or density 1 year prior to birth pulse ($r = -0.33$, $n = 26$, Fig. 5.19).

The 5 data points with highest mortality and lowest density were for 1973-1977, when factors other than forage, density, or deer condition apparently influenced fawn mortality. When those years were excluded, a more general increase of mortality with density was apparent. However, even that relationship depended mostly on data points for the very highest and lowest densities; mortality was extremely variable through the middle range of densities. Other information suggested that data points at both low and high densities were influenced by coincident environmental conditions rather than by deer density.

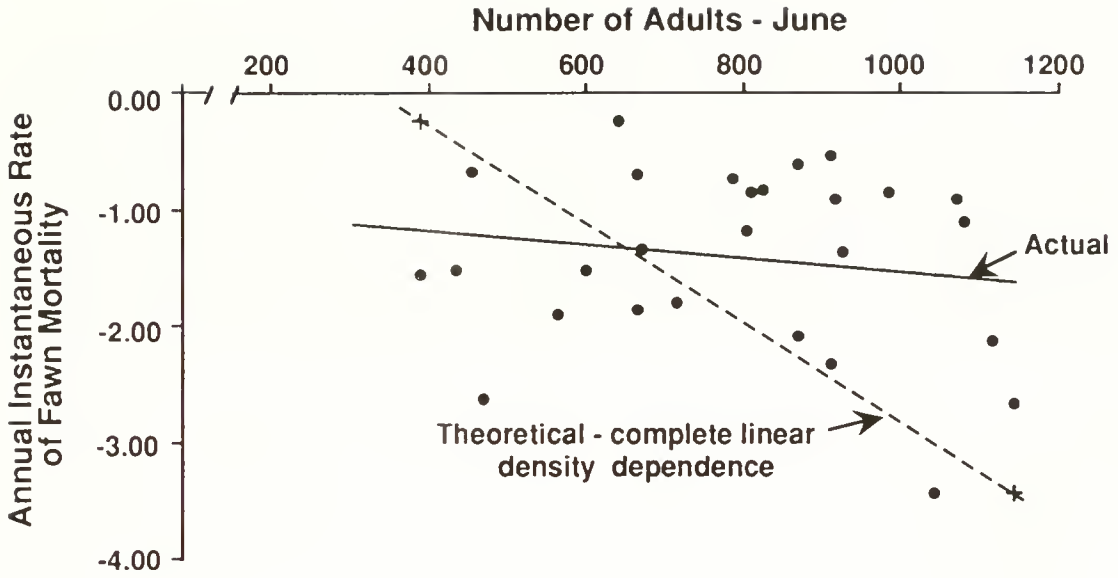


Figure 5.18. Annual instantaneous rate of fawn mortality plotted against the number of adults in the population at birth pulse. Solid line is the actual regression line, the dashed line represents theoretical complete linear density-dependent mortality.

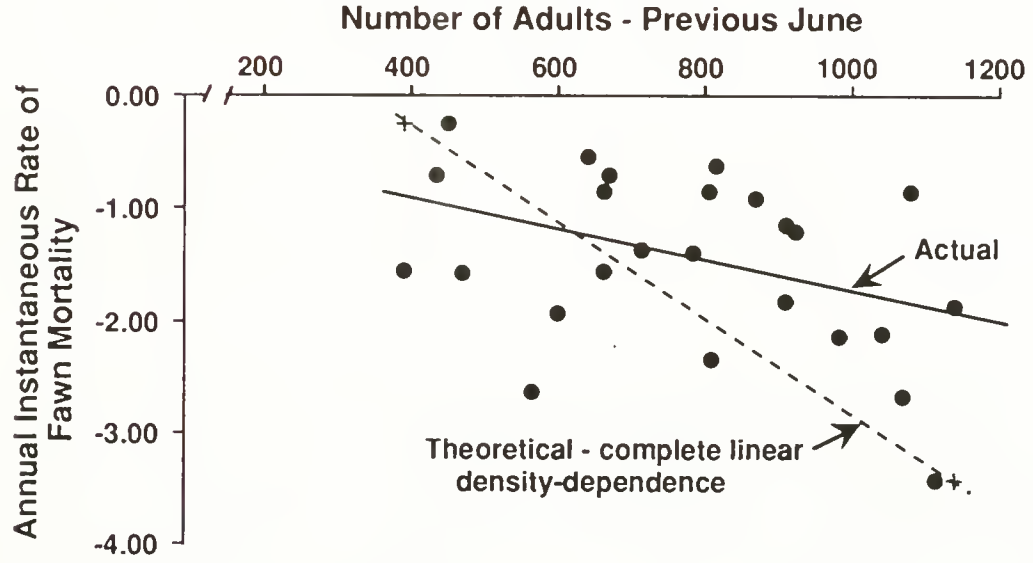


Figure 5.19. Annual instantaneous rate of fawn mortality plotted against the number of adults in the population 1 year prior to the birth of the measured cohort. Solid line is the actual regression line, the dashed line represents theoretical complete linear density-dependent mortality.

Numbers of recruits, rather than recruitment or mortality rate, must be plotted in order to determine the theoretical level of maximum sustained yield (MSY). If complete, linear density-dependent recruitment rates applied, the maximum number of recruits would occur at the peak of a parabolic yield curve. The yield curve shown in Figure 5.20 was plotted with the following assumptions: 1) the highest observed recruitment rate occurred at the lowest observed density, 2) the lowest observed recruitment rate occurred at the highest observed density, and 3) the relationship was directly linear.

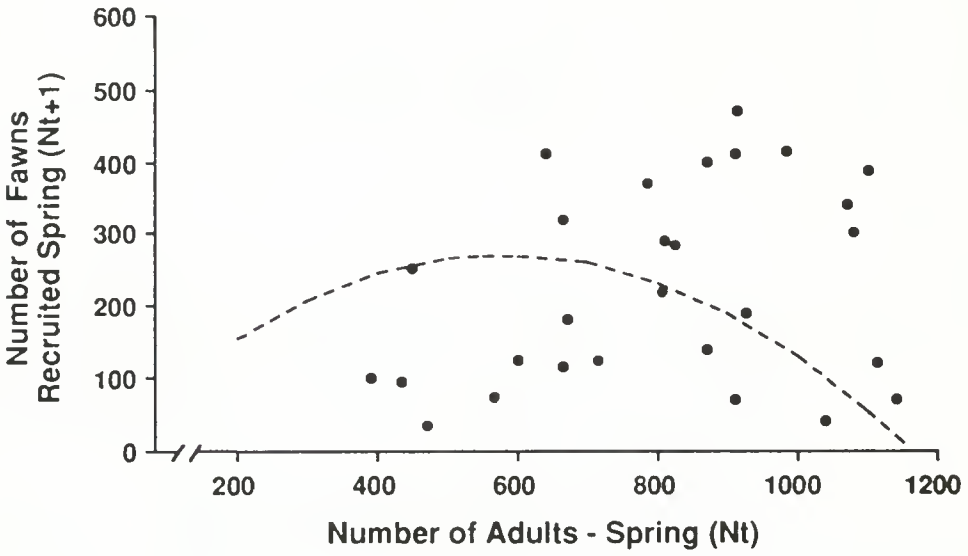


Figure 5.20. Yield in number of fawns recruited to 31 May plotted against the number of adults in the population on the previous 1 June. Dashed curve represents theoretical yield curve assuming complete linear density-dependent survival.

Yield in fawns recruited to 1 year of age plotted against the number of adults in the population at birth pulse (Fig. 5.20) indicated that recruitment did not occur in a linear density-dependent manner. If complete, linear density-dependent recruitment occurred, all points plotted should lie near the yield curve. As can be seen, yield was much below "expected" levels at low densities and much greater than "expected" at high densities. Within the observed range of densities, maximum yield occurred at population levels almost double those predicted by complete, linear density-dependent recruitment. Although a maximal yield curve for those data is drawn in Figure 5.20, it is apparent that they do not closely follow any pattern. Yield was quite variable at all observed density levels. There was also no

strong density-dependent relationship apparent when a 1 year lag in yield was plotted against deer numbers (Fig. 5.21) or when yield was plotted against numbers of females rather than numbers of adults.

It is apparent from the empirical data that deer density was not a reliable predictor of recruitment rates, survival rates, or yield for this population. Although some density relationships may exist, apparently the variability of other influencing factors (second-order effects, cf. Caughley 1981b) most often override potential density effects.

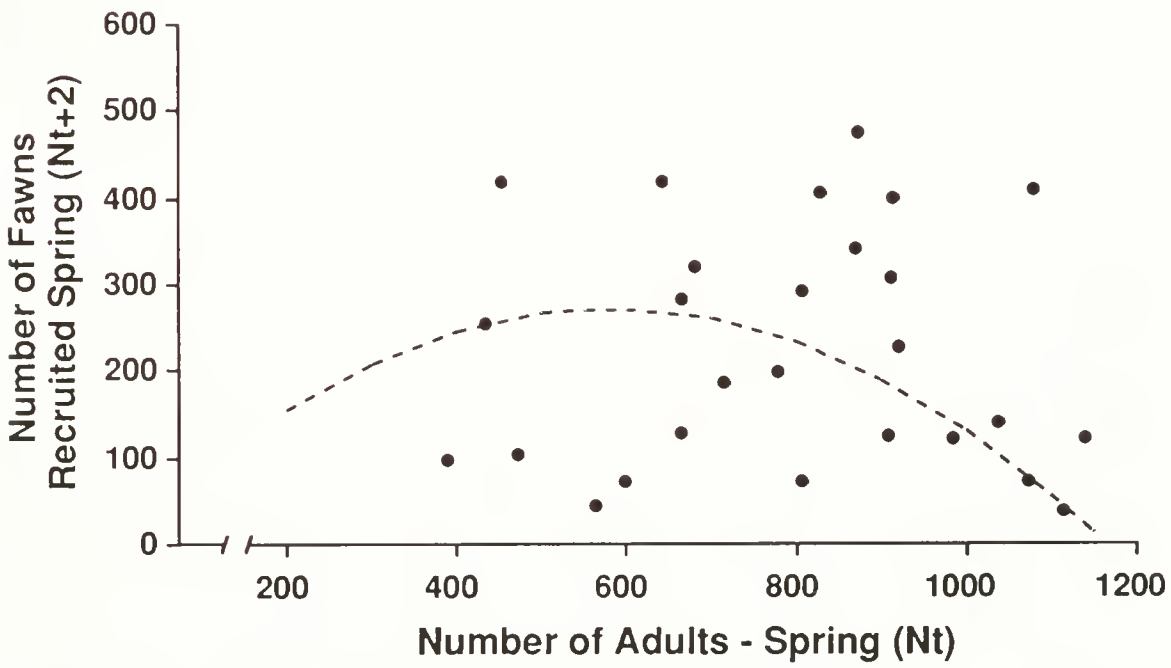


Figure 5.21. Yield in number fawns recruited to 31 May plotted against the number of adults in the population on 1 June, 2 years prior to fawn recruitment. The dashed line represents the yield curve assuming complete linear density-dependent survival.

CHAPTER 6

ADULT MORTALITY

Mortality Estimates

Several methods were used to estimate mortality during 1976-1986: loss of marked deer, change-in-ratio, harvest surveys, and differences between seasonal population estimates. Prior to 1976, differences between population estimates and harvest surveys were generally the only methods available, though change-in-ratio techniques could also be used during some years in the early 1960s.

Each approach had some deficiencies. For example, only small samples of marked deer were available during 1976-1979 and one death could make a 10-20% difference in estimated mortality rate. Estimates based on those data were considered only a general indication of high, moderate, or low mortality. Regular capture and marking and increased samples each year from 1979 through 1983 made mortality estimates based upon marked deer more credible. After 1983, field work was less intensive, few new deer were marked, and existing marked deer came to represent an older age structure more susceptible to mortality than the actual population. Those data tended to overestimate mortality rates.

Mortality estimates based on change-in-ratio are dependent upon accurate field classifications (Conner et al. 1986). Although early winter classifications based on observation of 60-80% of deer on the area were considered accurate, summer-autumn classifications may have under-represented females with fawns. Male:female ratios were always higher in July than September-October. Females became progressively more observable through summer and autumn, but they may not have been equally observable as males during some early preseason surveys. Also during some years, relatively small samples of hunter-killed deer were available to determine proportions of males and females harvested.

Despite these considerations, the 3 estimates calculated each year during 1976-1986 (Table 6.1) collectively provided a reasonable range. Within that range, the final estimates for all seasons and years (Tables 6.2 and 6.3) were those which best fit observed populations trends.

Female Mortality Patterns

Annual mortality of adult females ranged from 2.2 to 43.0% and averaged 17.2% (Table 6.2). An average of 11.0% (0-29.8%) of adult females alive on 1 June died during summer

Table 6.1. Mortality rates of adult deer 1976-1986, determined from marked deer, change-in-ratios, and population estimates.

	Adult Females									Adult Males	
	Annual			01 June - 01 December				01 Dec. - 31 May			01 June - 01 Dec.	
	N	Marked Deer	Pop. Model	N	Marked Deer	CIR[a]	Pop. Model	N	Marked Deer	Pop. Model	CIR	Pop. Model
1976-77	6	0.167	0.121	6	0.000	0.001	0.035	11	0.091	0.089	0.028	0.150
1977-78	13	0.154	0.049	13	0.077	0.002	0.016	12	0.083	0.033	0.530	0.500
1978-79	11	0.000	0.105	11	0.000	0.002	0.030	27	0.037	0.046	0.350	0.174
1979-80	39	0.077	0.059	39	0.000	0.002	0.012	45	0.022	0.048	0.453	0.488
1980-81	50	0.020	0.038	50	0.020	0.003	0.018	49	0.000	0.010	0.478	0.532
1981-82	68	0.221	0.191	68	0.132	0.126	0.118	69	0.130	0.083	0.585	0.580
1982-83	68	0.221	0.171	68	0.206	0.180	0.157	68	0.029	0.017	0.568	0.561
1983-84	66	0.273	0.114	66	0.091	0.039	0.019	67	0.179	0.129	0.313	0.246
1984-85	53	0.226	0.138	53	0.094	0.099	0.072	47	0.128	0.071	0.386	0.321
1985-86	40	0.075	0.022	40	0.000	0.015	0.015	40	0.075	0.008	0.265	0.385

[a]CIR=change-in-ratios

Table 6.2. Annual and seasonal turnover of adult females as a proportion of 1 June adult female population, 1960-1986, Missouri River Breaks, Montana.

	Recruitment[a]	Mortality[a]		
		1 June-31 May Annual	1 June-1 Dec. Hunting[b]	1 Dec.-31 May Winter
1960-61	0.346	0.187	0.168	0.019
1961-62	0.153	0.331*[c]	0.298*	0.033
1962-63	0.216	0.235*	0.196	0.039
1963-64	0.290	0.170	0.140	0.030
1964-65	0.063	0.214*	0.125*	0.089*
1965-66	0.126	0.158*	0.116	0.042
1966-67	0.196	0.207	0.163	0.044
1967-68	0.352	0.176	0.121	0.055
1968-69	0.262	0.206	0.131	0.075
1969-70	0.354	0.150	0.106	0.044
1970-71	0.250	0.154	0.088	0.066
1971-72	0.047	0.430*	0.182*	0.248*
1972-73	0.120	0.272*	0.174*	0.098
1973-74	0.154	0.244*	0.180*	0.064
1974-75	0.099	0.225*	0.169*	0.056
1975-76	0.048	0.113*	0.000	0.113*
1976-77	0.172	0.121	0.035	0.086
1977-78	0.148	0.049	0.016	0.033
1978-79	0.373	0.105	0.030	0.075
1979-80	0.353[d]	0.059	0.012	0.047
1980-81	0.273[d]	0.036	0.018	0.01
1981-82	0.221	0.191	0.118	0.073
1982-83	0.300	0.171	0.157	0.014
1983-84	0.076	0.114*	0.019	0.095*
1984-85	0.026	0.138*	0.072*	0.066*
1985-86	0.104	0.022	0.015	0.007
Mean	0.197	0.172	0.110	0.062
Range	0.026-0.373	0.022-0.043	0.000-0.298	0.014-0.248

[a] Recruitment and mortality expressed as a proportion of starting, 1 June population. Recruitment equals number of yearling females 31 May/number adult females previous 1 June. All mortality expressed as number of adult females lost during the period/number of adult females 1 June, at start of year.

[b] The period 1 June-1 Dec., called Hunting Mortality, also includes minor numbers (based on marked deer) of deer dying from causes other than hunting.

[c] * - Indicates that mortality during the period exceeded annual recruitment.

[d] Recruitment was actually 0.482 for 1979-80 and 0.336 for 1980- 81, but because of emigration of yearling females, recruitment to the population was at the figures listed in the table.

Table 6.3. Annual and seasonal turnover of adult males as a proportion of 1 June adult male population, 1960-1986, Missouri River Breaks, Montana.

	Recruitment[a]	Mortality[a]		
		1 June-31 May Annual	1 June-1 Dec. Hunting[b]	1 Dec.-31 May Winter
1960-61	0.740	0.520	0.500	0.020
1961-62	0.311	0.344*[c]	0.311	0.033
1962-63	0.373	0.322	0.288	0.034
1963-64	0.468	0.339	0.323	0.016
1964-65	0.100	0.414*	0.343*	0.071
1965-66	0.271	0.396*	0.354*	0.042
1966-67	0.429	0.429	0.405	0.024
1967-68	0.762	0.381	0.357	0.024
1968-69	0.500	0.448	0.397	0.051
1969-70	0.656	0.377	0.344	0.033
1970-71	0.436	0.423	0.372	0.051
1971-72	0.089	0.570*	0.456*	0.114*
1972-73	0.293	0.268	0.244	0.024
1973-74	0.310	0.310	0.286	0.024
1974-75	0.191	0.429*	0.357*	0.072
1975-76	0.125	0.500*	0.469*	0.031
1976-77	0.500	0.200	0.150	0.050
1977-78	0.385	0.500*	0.500*	0.000
1978-79	1.087	0.174	0.174	0.043
1979-80	0.954	0.488	0.488	0.024
1980-81	0.661	0.532	0.532	0.016
1981-82	0.435	0.580*	0.580*	0.029
1982-83	0.719	0.561	0.561	0.018
1983-84	0.185	0.246*	0.246*	0.077
1984-85	0.071	0.321*	0.321*	0.054
1985-86	0.359	0.385*	0.385*	0.025
Mean	0.439	0.413	0.375	0.038
Range	0.071-1.087	0.174-0.580	0.150-0.580	0.000-0.114

[a] Recruitment and mortality expressed as a proportion of starting, 1 June population. Recruitment equals number of yearling males 31 May/number adult males previous 1 June. All mortality expressed as number of adult males lost during the period/number of adult males 1 June, at start of year.

[b] The period 1 June-1 Dec., called Hunting Mortality, also includes minor numbers (based on marked deer) of deer dying from causes other than hunting.

[c] * - Indicates that mortality during the period exceeded annual recruitment.

-autumn and 6.2% (<1-24.8%) died during winter-spring. Overwinter mortality rates based on numbers of females alive on 1 December were slightly higher, averaging 7.1% and ranging from <1% to 30.3%.

Most summer-autumn mortality of adult females occurred during the hunting season. Only 5 (12.5%) of 40 deaths of marked females for that period were attributed to causes other than hunting. Because hunting during 1975-1980 was for males only, all mortality of females during autumn of those years ($\bar{X}$ = 1.9%) resulted either from natural causes or illegal kills.

Total annual mortality of adult females exceeded recruitment of yearling females during 11 of 26 years (Table 6.2). Harvest alone was sufficient to reduce the population during 7 years: 1961, 1964, 1971-1974, and 1984. During 1964 and 1984, annual harvest rates were below the long-term average recruitment rate, but annual recruitment was much below average. Harvest rates were near the average recruitment rate during 1971-1974, but annual recruitment was below average each year. Harvest rate exceeded the long-term average recruitment rate for females only in 1961.

Mortality during winter, alone, was sufficient to reduce the adult female population during 1964-65, 1971-72, 1975-76, 1983-84, and 1984-85. During 1962-63 and 1965-66, the combination of hunting and winter mortality was greater than recruitment. In 1964-65, 1971-72, and 1984-85, both hunter harvest and winter mortality exceeded recruitment. However, winter loss was greater than average recruitment only during 1971-72.

Based on average recruitment rates and the theories of compensatory mortality and recruitment, hunting mortality of adult females was excessive only during 1961. During 3 periods, 1964-1965, 1971-1976, and 1983-1985, however, annual recruitment was much below the long-term average and compensatory mortality and recruitment did not operate according to theory. Thus, the use of average recruitment rates and the theories of compensatory mortality and recruitment did not provide a viable basis for determining sustainable harvests of adult females.

Male Mortality Patterns

Annual mortality for adult males averaged 41.3% (Table 6.3), more than twice the rate for adult females. Annual mortality ranged from 17.4% (1978-79) to 58.0% (1981-82). Mortality from hunting averaged 37.5%, more than 3 times the average for adult females. Winter mortality, however, averaged only 3.8%, about half that for females. The highest rate of winter mortality for males was 11.4% during 1971-72.

Total annual mortality for adult males also exceeded recruitment rates during 11 of 26 years; however, 3 of those years were different from those observed for females. Hunter harvests exceeded annual recruitment during 10 years and equalled it during one (1961-62). Similar to females, hunter harvests were generally not excessive in any year, if based on long-term average recruitment. During 7 of 11 years of population decline for males, however, recruitment rates were much below the long-term average.

The lower rates of winter loss for males than females indicated that hunter harvests were less additive to other forms of mortality for males than for females. Because of the rut, adult males normally entered winter in poorer condition than other deer and their mortality rate during winter was expected to be high. However, because of heavy (>50%), selective harvests of older and larger males, many of those most likely to be in poorest condition after the rut were not present during winter. The males least likely to be shot, yearlings and mature animals that were not dominant breeders, were those most likely to enter winter in better condition, with the best chance of survival.

Causes of Mortality

Females

Two major causes of adult female mortality were identified: hunting and coyote predation. Of 77 marked adult females known to have died during 1976-1986, 26 (34%) were shot, and 6 others (8%) were presumed shot but not reported, based on time of disappearance and other evidence. Thus, a total of 42% of adult female mortality was categorized as hunting-related. Five (19%) of the 26 certain hunting-related deaths, were either crippling losses or illegal kills. Only 1 was known to have been illegally shot, though it is possible that some classified as crippling loss were intentionally left in the field.

Nine deaths (12%) resulted from coyote predation during winter and early spring. Additionally, 27 deaths (35%) for which cause of death was not ascertained, occurred during winter-spring. Predation was ruled out in 2 of those, but was suspected to be the proximal cause of death for the remainder. All mortality of unmarked deer during winter-spring, for which cause was determined, was the result of coyote predation. Additionally, almost all mortality of marked white-tailed deer on the river bottoms adjacent to our study area and mule deer on the uplands of the NCRCA study area during winter 1975-76 was attributed to coyote predation (Knowles 1976).

Nine marked females (12%) died during summer and autumn, 2 as a result of coyote predation and 7 of unknown causes.

Males

Hunting was known or suspected as the cause of 91% of all deaths of marked adult males during 1976-1986. Of 46 known to have died, 32 (70%) were shot or crippling losses and 10 (22%) were suspected hunting mortalities based on time of disappearance. Additionally, almost all loss of males determined from population estimates (Table 6.3) occurred during the hunting season. Of 32 marked males verified shot, 2 (6%) were crippling losses. Only 4 (9%) males died during winter-spring. Cause of death was not assigned because the remains were not found. Though coyote predation was suspected as the proximal cause, wounding during the hunting season may have often been the ultimate cause. That was the case for 1 marked male assigned to the hunting loss category. He was wounded during hunting season and killed by coyotes during February.

Age-specific Mortality

Females

Age-specific mortality rates were determined for 118 1-year-old and older females over 404 deer-years (Fig. 6.1). Only females aged to a specific year class at capture and those marked at the beginning of a biological year were included in the sample. Age-specific mortality was categorized as either hunting or natural. The few females that were suspected but not verified as being shot were included as hunting mortalities. Natural mortality included all other causes; most occurred during winter and spring.

Total annual mortality was highest for females aged 12 and older, followed by females between the ages of 6 and 7, 9 and 10, and 1 and 2 years of age (Fig. 6.1). Relatively high mortality rates for the youngest and oldest adults were not unexpected, but high mortality rates for females in their 7th year of life was surprising. Most of the latter occurred during winter and was not hunting related (Fig. 6.1). As we noted elsewhere (Hamlin and Mackie 1987), the increased mortality for 6 year-old females was an aberration from the typical U-shaped mortality curve of mammals (Caughley 1966). The coincidental peaks in survival of fawns to 6 months and female mortality at 6 years suggested a relationship between reproduction and mortality. We hypothesized (Hamlin and Mackie 1987) that the peak in non-hunting mortality rate at 6 years was the average outcome of cumulative reproductive stress resulting from a strategy of maximum reproductive effort each year in a variable, unpredictable environment.

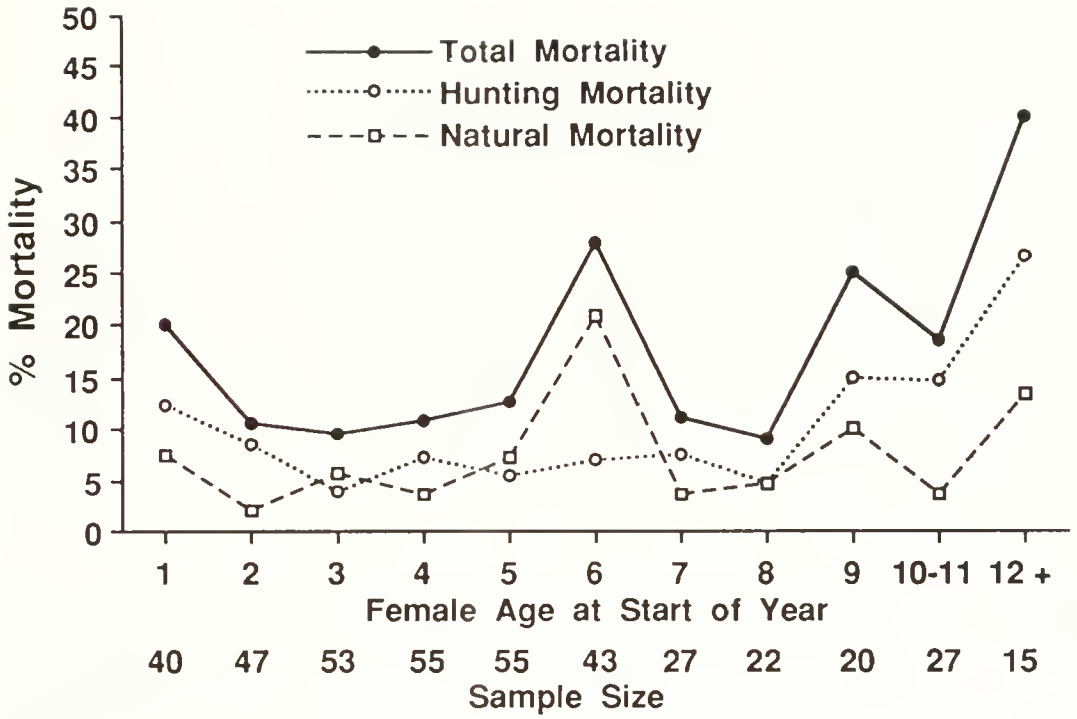


Figure 6.1. Age-specific mortality rates for female mule deer in the Missouri River Breaks, Montana, 1976-1986.

Except in the very best years, lactating and rearing fawns to 6 months of age probably draws on body reserves in addition to nutrition provided by current forage. Forage quality is often insufficient to fully replace body reserves following weaning, and on average, body reserves have reached a critical level following weaning in the fifth reproductive year. The more fawns a female has recruited during her first 5 reproductive years (cumulative reproductive stress), the poorer her condition at age 6 and the greater her vulnerability to death. Many females that do not die at 6 years either do not have fawns the next year or lose them shortly after parturition. This gives them the opportunity to recover body reserves, such that survival and fawn recruitment among 8+ year olds improves over that at 6 years.

Reproductive histories were available for 7 of 9 females that died between age 6 and 7 from non-hunting causes. All had recruited fawns to weaning age at above average rates during the years leading up to their death. Four of the 7 had weaned fawns during the year of their death and for at least 2 years prior to that. The reproductive status for 2 was unknown during the year of their death, but they had both weaned fawns for at least the 2 years prior to their death.

One had weaned fawns during the year of her death and for at least 1 of 2 prior years.

Although mortality of adult females was unusually high for 6 year old females in our sample, reproductive history rather than age, per se, may be the operative factor in reproductive "burnout". Marked females of all ages that died from non-hunting causes during the study had been much more (X^2=26.1, 1 d.f., P>0.001) productive prior to their death than marked females that did not die, or died from hunter harvest. Twenty-eight 2+ year old females that died of non-hunting causes recruited fawns to weaning age during 76 (89%) of 85 observed opportunities prior to their death. Marked females that did not die, or were harvested, recruited fawns to weaning age during only 57 (55%) of 103 observed opportunities.

On an individual basis, the relationship of high productivity and relatively early mortality is not perfect. At least some females were very productive for 5-6 years and have not yet died. On the average however, high productivity appeared to place the female at greater risk of death. Circumstances during the period the female is highly productive probably influence the outcome. Females productive during favorable summer and winter conditions were probably less vulnerable than those that recruited their last fawn(s) substantially on body reserves during a dry summer followed by a severe winter. Clutton-Brock et al. (1982) also noted that for red deer females, mortality rates for productive females of all ages were higher than for non-productive females, especially after 10 years of age.

Hunting mortality rates were highest for females between 1 and 2 years of age and those 9+ years of age. No age-specific differences were apparent for females aged 3-8 years. Females with fawns generally occupied the most secure habitat. Yearlings, until they rejoined their mother's social group in late autumn or winter, were most likely to occupy areas on the fringes of their natal range or entirely new and unfamiliar home ranges. Thus, they were more likely to occupy relatively more open habitats where they were vulnerable to hunting. They also may be less wary than older deer.

The relatively high mortality of 9+-year-old females as a result of hunting was not expected. Limited evidence, based on a few marked animals, suggested that older females without fawns may have lost secure fawn-rearing habitat to younger, productive females. This placed them, like yearlings, in more open habitats where they were vulnerable to hunters. A combination of additional factors also may help explain the relatively high hunting mortality for older females. After 7 years of age, females may undergo an alternating cycle of fawn

production and subsequent poor condition with no fawn recruitment the following year. During years when they do not wean fawns, females would be more likely to occur in larger groups (Chapter 7) and be more vulnerable to hunters. Also, older females in general are likely to be in poorer condition, which may cause them to be less alert and to lag in groups fleeing from hunters.

In a non-hunted population, relatively high natural mortality rates would be expected for females 12-years-old and older. The relatively high hunting mortality for those females in this population removed many before they were exposed to natural mortality during winter. Thus, some hunting mortality of older females may not be additive to other mortality, thereby reducing observed natural mortality rates for older females to lower than expected levels.

Based on population estimates, emigration of yearling females was apparently not balanced by immigration. Although this loss was relatively minor in total and most occurred for the 1979, 1980, and 1986 cohorts, it increased loss of yearling females to the population. When all losses to the population, including emigration, are considered, mortality of yearling females was 25% rather than the 20% (Fig. 6.1) observed for individuals.

Males

Because only small samples of 3+ year old males were available to determine age-specific mortality rates and the samples did not show differences, males 3-years-old and older were combined. Mortality rate for 33 males between 1 and 2 years of age was 36%. Between 2 and 3 years of age, 50% of 28 males died, and annual mortality was 56% for 36 males 3-years-old and older.

As discussed previously, most deaths of adult males were hunting related. Only 9% of deaths of marked males were suspected to be the result of natural causes. The higher harvest rate of males aged 2 years and older than for yearlings apparently resulted from hunter selection for larger-antlered deer. Except for extreme drought years, most 2 year old males had small, 4X4-point antlers that were obviously larger than yearling antlers. Apparently, that antler size was enough to satisfy many hunters, because mortality rate of older and larger males did not increase substantially after 2 years of age. The fact that the mortality rates of 3 year old and older males did not increase beyond that of 2 year old males may also be related to older males being more wary than younger ones, at least prior to the rut.

Antler size of younger males also influenced relative harvest rates, depending on the structure of the general hunting season. During hunting seasons when only antlered males were legal game, a significantly greater proportion of yearling males with 2 antler points or more per side were harvested than occurred in the post-season population (X^2=9.39, df=2, P=0.01; Table 6.4). Although contributions of each antler class to the total chi-square value were similar, selection against "spike"-antlered yearling males provided the greatest contribution. During hunting seasons when any deer could be harvested on the general license (A-tag), the distribution of antler points per side for yearling males in the harvested sample was not statistically different from that of the post-season population (X^2=1.99, df=2, P= 0.39).

Table 6.4. Antler points per side of yearling males for harvested samples and post-season populations during antlered male only and any deer hunting seasons.

	Number of Antler Points					
	Male Only Seasons[a]			Any Deer Seasons[b]		
	1X1	1X2	2X2+	1X1	1X2	2X2+
Harvest Sample	6 (0.08)[c]	4 (0.05)	66 (0.87)	52 (0.22)	22 (0.09)	166 (0.69)
Post-Season Classification	41 (0.18)	29 (0.13)	155 (0.69)	136 (0.24)	66 (0.12)	363 (0.64)

[a] 1976-80 and 1985 and 1986
[b] 1960-64, 1971, and 1981-84
[c] Number (proportion)

Although there may be some hunter selection for larger-antlered yearling males during all years, the lesser degree of selection apparent during any-deer seasons may, at least partially, result from small antlered "spikes" being shot as antlerless deer (Wood 1987). Conversely, during antlered male-only seasons, many "spikes", especially those some distance away, may not be perceived as males, thereby lowering their harvest rate.

Dispersal may have affected mortality rates of yearling males. Only 6 (29%) of 21 yearling males that remained within the population were shot, while 6 (50%) of 12 yearling males that left the area were shot. Some of the yearling males that left the population unit and were shot had dispersed into obviously less secure habitat. Others, however, dispersed to

habitat that was not structurally different or obviously less secure than that from which they had dispersed. For those males that lived to 2 years of age, there was no apparent difference in known age at death between those remaining in the population ($\bar{X}$ = 3.6, n=12) and those that left the area ($\bar{X}$ = 3.5, n=5).

Based on population estimates, emigration and immigration for yearling males apparently balanced during most years, so dispersal did not contribute additional mortality to the population.

Effect of Home Range Location on Mortality and Productivity of Females

Because of indications that deer inhabiting parts of the study area with low topographic relief experienced greater mortality during winter than deer on other parts of the area, we examined the relationships between home range location and mortality and productivity of marked females. Home range and movements data (see Chapter 8) indicated 2 basic movement patterns for females: resident and migratory. Migratory deer most often occupied areas of low topographic relief during summer and moved at least 3 km to areas containing steeper terrain during autumn or winter. Some resident deer inhabited areas with low topographic relief yearlong, but most had home ranges that included at least some steep terrain comprised of north- and south-facing slopes. For analysis, low relief terrain was defined as those areas occupied during summer by marked migratory deer and all areas of equal or lesser relief.

Mortality rates of marked females were examined during 3 winters of relatively high mortality (1981-82, 1983-84, and 1984-85). Data from prior winters were not included because few deer were resident to areas of low relief during population lows, and few of those were marked. Mortality rates were compared among 3 movement and home range categories: resident yearlong in areas with low topographic relief; occupying areas of low relief during summer but migrating to areas of steep terrain during autumn or winter; and resident yearlong in areas that contained some steep north- and south-facing slopes.

Of 69 marked adult females that entered winter 1981-82, 9 (13%) died or disappeared and never were reobserved. In 1983-84, 12 (18%) of 67 marked adult females died, and in winter 1984-85, 6 (13%) of 47 marked females died. For the 3 winters combined, 27 deaths occurred (15%) over 183 marked adult female-winters.

Mortality rates were significantly different among the 3 categories of home range use (X^2=16.1, P<0.01, 2 df).

Eighteen (29%) of 62 females resident in areas of low topographic relief died. Only 1 (3%) of 37 migratory females and 8 (9%) of 85 females resident in areas that contained steep terrain with north- and south-facing slopes died. Females resident yearlong in areas of low topographic relief not only died at the highest rate overall, but also in each winter. When they were compared to all other females that used steeper terrain, whether resident or migratory, the difference in mortality rates remained significant (X^2=13.8, P<0.001, 1 df).

There are several probable explanations for the higher winter mortality rates of females resident in areas of low topographic relief than for other females. During late summer and autumn, succulent forage was scarcer in areas of low relief than in steeper terrain both because of more intensive cattle grazing and because the shallow drainages were less protected from the desiccating effects of sun and wind. These areas also had less topographic and microsite diversity and therefore less diversity of plant species and plant phenology than areas of greater topographic relief. Thus, deer resident to areas of low topographic relief had shorter periods of access to high quality forage than other deer and females probably experienced more lactation stress, especially during dry summers. During winter, these deer had to spend more energy moving through deeper snow because of the lack of bare south-facing slopes and large, thickly-timbered, snow-intercepting north-facing slopes. Also, they did not have access to large, warmth-radiating south-facing slopes and the diversity or quantity of winter forage available in steeper, more diverse areas. Overall, deer resident to areas of low relief had a shorter period of positive energy balance and a longer, more severe period of negative energy balance than deer occupying areas with more diverse topography. They were more susceptible to all sources of natural mortality including coyote predation and malnutrition.

We expected that in areas of low relief, fawn production and survival should be relatively low, and total deer numbers lower than on areas with greater topographic relief. This generally appeared to be the case, but because of the variability in movements of migratory deer between areas of low and high relief, interpretation of the data was difficult.

At least some of the higher surviving migratory females had not moved to areas of steeper terrain at the time of some early winter surveys and some had not moved back to areas of low relief at the time of some spring surveys, thus fawn survival and total deer numbers in areas of low relief was difficult to determine. Also, if females in low relief areas died at a greater rate than other females during winters of high mortality, fawn survival for original numbers of females

in areas of low relief would be lower than apparent in sex and age classification data. Despite these considerations, which minimize differences in classifications, fawn survival was generally poorest in areas of low relief during both early winter and spring (Fig. 6.2). However, during years of higher fawn survival, fawn survival was as high or higher in areas of low relief as in areas of greater topographic relief.

Numbers of adult females observed in areas of low relief during early winter helicopter surveys declined earlier and recovered later than in areas of greater relief. Numbers in areas of low relief declined from 1970 through 1978 and started to recover by 1979 (Fig. 6.3). The number of females in areas of greater relief did not decline until 1972, reached a low during 1976, and began to recover in 1977, 2 years earlier than in areas of low relief. The number in areas of low relief reached a peak in 1981 and declined following mortality during the winters of 1981-82, 1983-84, and 1984-85 (Figure 6.3). On the other hand, females in areas of greater topographic relief continued to increase through 1984 and then declined. These data substantiate those provided by marked deer in that deer numbers in areas of low relief were most affected during winters of relatively high mortality. These data are not precise comparisons because some year-to-year fluctuations in relative numbers between areas could have resulted from changing proportions of migratory females in the 2 areas at the time of the surveys and changes in relative observability between years.

Relative numbers of total deer in the 2 types of habitat during spring were even more difficult to interpret than numbers during early winter. This occurred because there was even more variation between years in the location of migratory females at the time of spring surveys. During spring 1978, 1979 and 1982 (after severe winters) most migratory females remained in areas of high topographic relief through the time of spring surveys. During those years, total numbers of deer using areas of low relief during spring were underestimated, and numbers using areas of high relief were overestimated. The data (Fig. 6.4) do indicate, however, that there were very few deer resident yearlong to areas of low relief during 1978 and 1979. After 1982, spring surveys were flown later than previously and most migratory females had returned to areas of low relief at the time of the surveys. Although not ideally controlled, the data seemed sufficient to indicate that numbers of deer in areas of low relief decreased more than those in areas of greater relief. This differential decline occurred both during the population low of the mid-1970s and the population decline from winter 1983-84 through spring 1986.

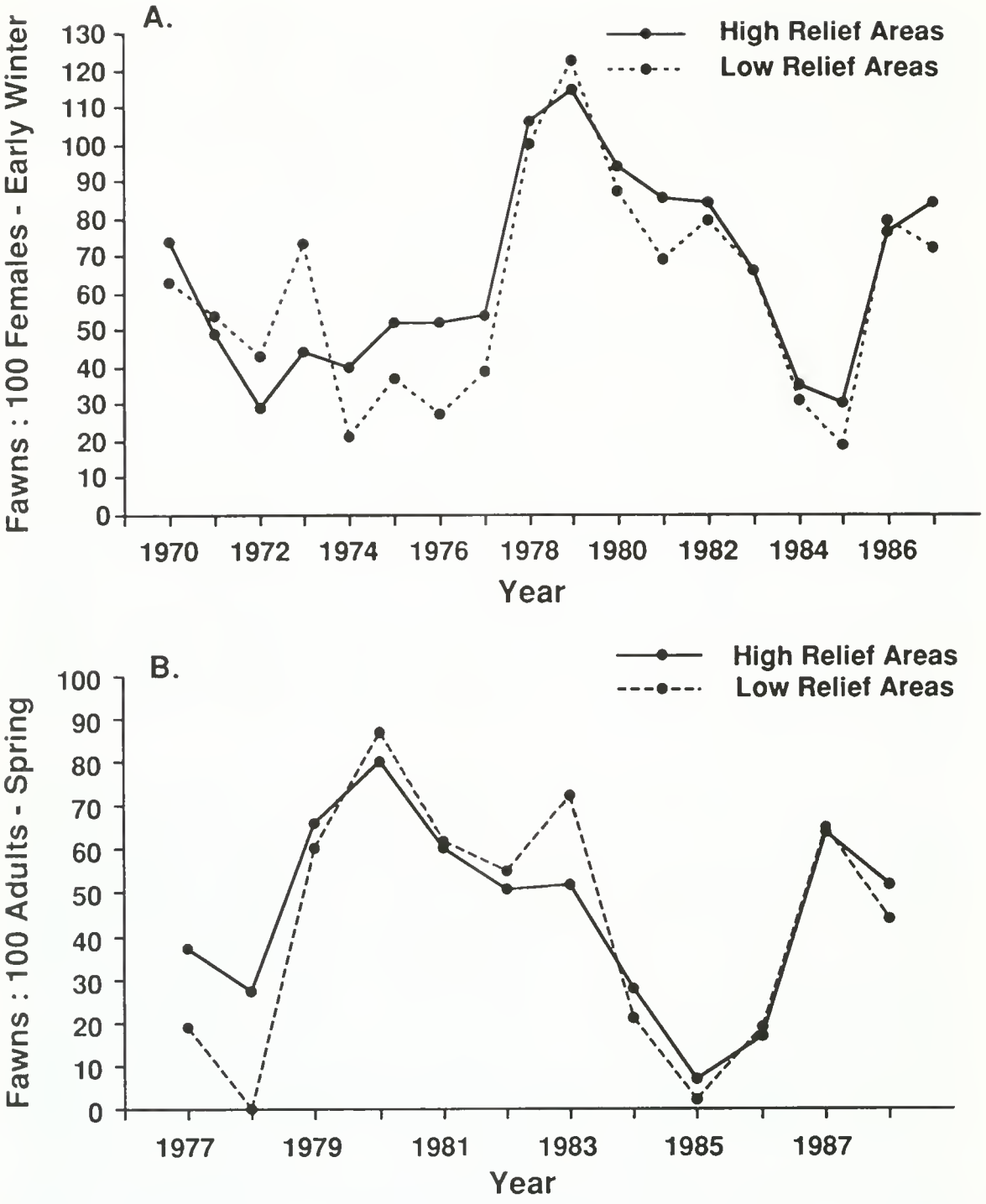


Figure 6.2. Fawns:100 females during early winter (A) and fawns:100 adults during spring (B) compared with between high relief terrain and low relief terrain.

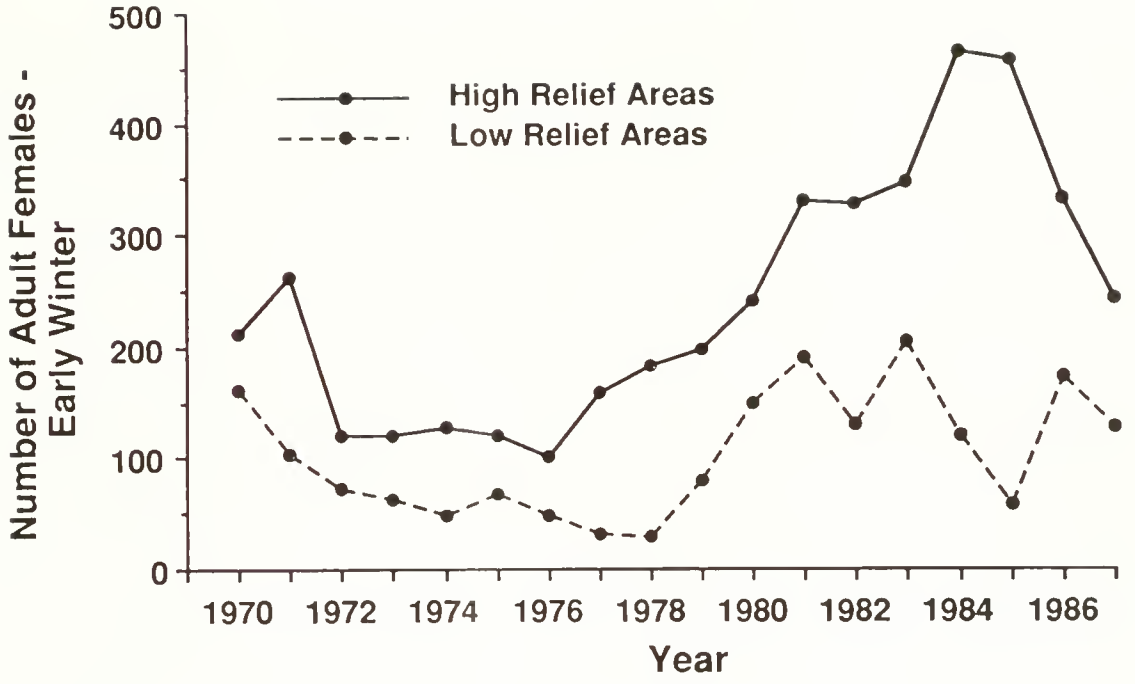


Figure 6.3. Number of adult females observed during early winter helicopter surveys compared between high relief terrain and low relief terrain.

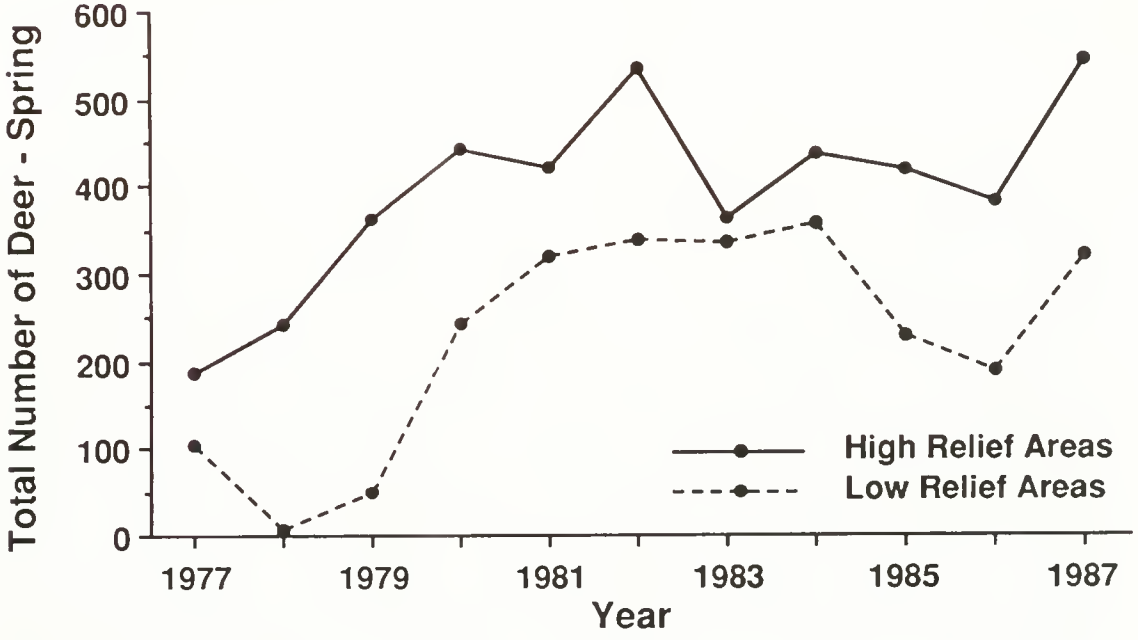


Figure 6.4. Number of mule deer observed during spring aerial surveys compared between high relief and low relief terrain.

Our data indicated that natural mortality and fawn production of adult females not only varied by age among individuals, but also varied across the area depending upon the specific strategy of habitat use by deer or location and characteristics of habitat within each home range. Areas with low topographic relief did not provide good survival habitat for mule deer across the observed range of environmental variability. Deer could survive and reproduce well on these areas during favorable periods but were more vulnerable to mortality during dry years or cold winters with deep snow.

We also suspected that hunting mortality might be higher for females occupying more open, low relief terrain, but apparently that was not the case. Mortality rate of females owing to hunting was not significantly different among the 3 home range categories (X^2=1.27, P=0.54, df = 2). The fact that we did not find that females in the more open, low relief areas more vulnerable to hunting may be related to the coincident lower accessibility of those areas. Most of the broad areas of low relief occurred in the southwestern and southcentral portions of the area, relatively distant from major roads. Access roads crossed large areas of habitat unsuitable for deer before reaching hunting areas. Hunters often bypassed open, low relief areas, preferring to travel on major trails until more typical deer habitat was reached. Thus, a substantial portion of low relief terrain received only minor hunting pressure. Our data did not allow us to determine if more deer were shot in low relief portions of generally high relief areas.

Comparative Effects of Hunting on Females and Males

Because of the normally lower proportion of males than females in the adult population, total numbers of males are lower than those of females and hunting mortality can have a different effect on male and female populations. Hunting of males occurred annually, so natural mortality rate for males in its absence remains unknown. If, in the absence of hunting, the natural mortality rate of males is higher than for females as observed by others (Martinka 1978, Gavin et al. 1984, Kie and White 1985), it may not be possible to maintain adult sex ratios much higher than 40-60 males:100 females. Based on our data, it should be possible to maintain post-season ratios of 20-35 adult males:100 adult females during most years without restricting the number of people hunting males. If hunting pressure increases, however, this expectation may be unrealistic. Following years of unusually poor fawn recruitment, unrestricted hunting of males resulted in post-season ratios of less than 20 males:100 females.

Past regulations have allowed hunters to select heavily for adult males, which were harvested at a rate 3-4 times

greater than adult females. Because male populations are lower than female populations and recruitment adds proportionally greater numbers to the male population, the male population can sustain a higher mortality rate (but not numbers) than females and remain stable. The degree to which males can be harvested more heavily than females depends upon the fawn recruitment rate and post-season male:female ratio the manager would like to maintain.

As we have seen, neither fawn recruitment rates nor mortality rates of adults were stable, and averages were seldom useful for management decisions. A harvest strategy of quotas based on average recruitment and average natural mortality or constant hunting pressure would contribute to increased fluctuations of both males and females. Underharvests occur during periods of high recruitment and over-harvests during low recruitment (Beddington and May 1977). A "tracking strategy" (Caughley 1977) that accounts for annual variation could more successfully manage populations. The general season structure sets bag limits and sex restrictions on the A-tag (first tag) which an unlimited number of hunters can purchase over the counter. That season and its restrictions are set each year before winter survival is determined or a final estimate is made of the previous autumn's harvest. Thus, data used to establish the general season are 1 year behind and the efficiency of a "tracking strategy" is reduced. The number of B-tags (second tags specific for antlerless deer) can more closely "track" population trend because final quotas for the drawing of those tags are established after winter survival and the previous year's harvest have been determined.

A model that demonstrates maintenance of different post-season sex ratios of adults under varying fawn recruitment and adult mortality rates is illustrated in Figure 6.5. Conclusions from the curves reflect no significant compensatory reproduction or mortality in the population. If the post-season adult sex ratio was 20 males:100 females and if only 10 fawns were recruited per 100 females, any mortality over 20% for adult males during the following year reduces the male population and the male:female ratio to below 20:100 (Fig. 6.5). Because hunting mortality of adult males was almost always more than 20% under past regulations, a population decline for males over the next year can also be expected. If 50 fawns:100 females were recruited, the male population could sustain 55% annual mortality (near the highest observed) and maintain 20 males:100 females post-season. Annual mortality below 55% would result in the post-season sex ratio rising above an existing 20:100 and an increase in the number of males.

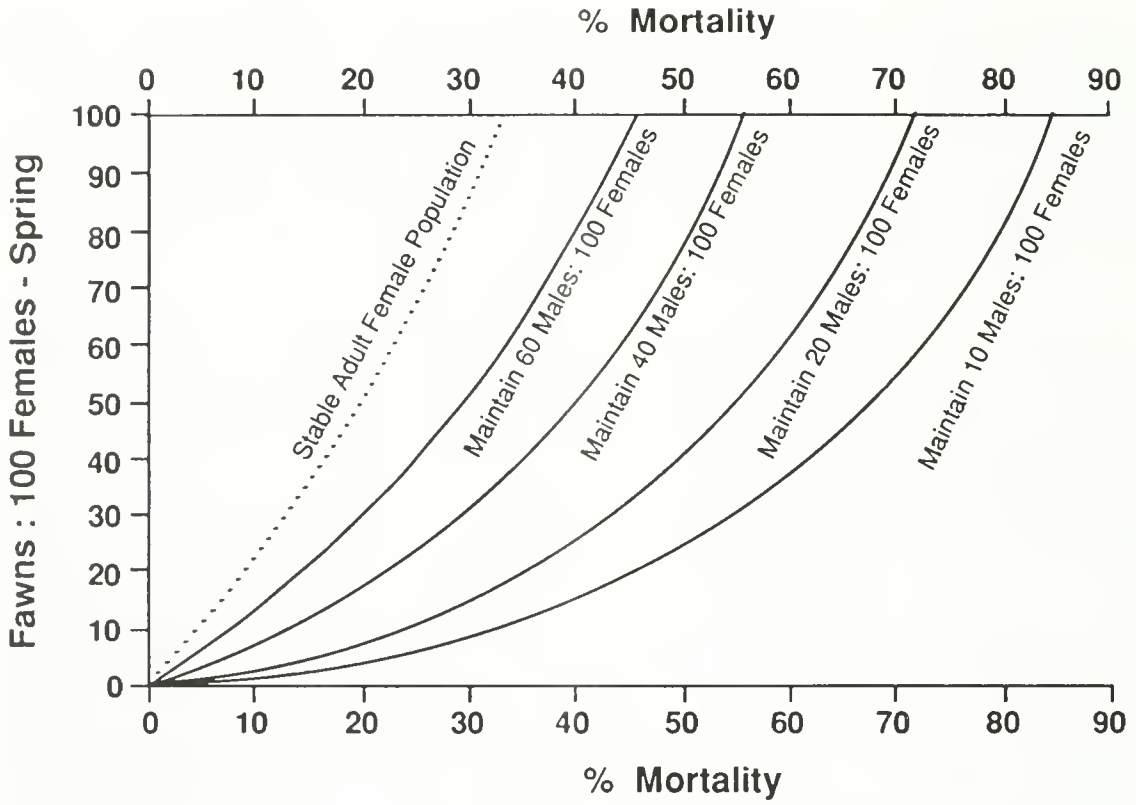


Figure 6.5. A simplified model illustrating adult female mortality rates that will maintain a stable female population and mortality rates for males that will maintain selected male:100 female ratios given various recruitment rates.

The model also indicates that within the normal range of adult sex ratios, stable populations of females cannot be maintained with a mortality rate similar to that of males. At 40 fawns recruited per 100 females, annual mortality rates for adult males of 25%, 33%, 50%, and 67% would maintain post-season sex ratios of 60 males:100 females, 40:100, 20:100, and 10:100, respectively. At the same recruitment rate, the female population would decline if annual mortality exceeded 17%. Fawn recruitment of at least 12-18 fawns:100 females is necessary to replace the average annual natural mortality rate of 6-8% for adult females. A harvest rate of 33% for adult females would have reduced the female population during all years 1960-1986, except 1979-80, when numbers would have roughly stabilized rather than continued to increase. Also, because female populations are larger than male populations, an equivalent harvest rate for the 2 sexes will result in a higher numerical harvest of females.

The importance of the information in Figure 6.5 is not in its precision, but that it can provide early insight to the likely effect of hunting regulations in a given year. If the goal is for the female population to increase, stay the same, or decrease and the fawn recruitment rate is known, the general level of antlerless tags, if any, necessary to achieve the objective can be estimated. It is also possible to determine when the male population is likely to decline, given general hunting of males. To keep the male population from declining or raise the male:female ratio, harvest of males may have to be restricted during some years of low recruitment.

Overall, allowable harvest rates for females, in the absence of compensatory reproduction and mortality, are generally lower than previously believed. Also, in most areas, we are either harvesting males at higher rates or total male mortality from all causes is higher than previously believed. The mule deer herd at Sage Creek in central Montana, for example, is characterized by recruitment generally greater than 50 fawns:100 females and post-season adult male:female ratios of 10:100 or less. This indicates that total annual loss of males to the population is usually 70-80%. Although it is probable that much of that mortality results from hunting, it also is possible that net emigration of yearling males from that open habitat contributes to high annual loss of males.

Chapter 7

SPATIAL AND SOCIAL DISTRIBUTION

Spatial Distribution

General Patterns

Generally, mule deer occurred throughout the study area. Thus, our analysis primarily relates to patterns of dispersion or the spatial distribution of individuals within the population (Pennak 1964). Spatial and temporal patterns and factors influencing dispersion were determined by plotting the locations of deer observed during 32 aerial surveys from autumn 1976 through spring 1984 within 953 28.8-ha blocks generated for the area. Prior to 1976, deer observed during aerial surveys were assigned to 1 of 10 multi-sized subdivisions of the area. Those locations and locations of deer observed along vehicle routes during 1960-1964 within 3.9 km^2 blocks (Mackie 1970) provided insight to general, long-term changes in distribution.

The general pattern of dispersion or intensity of use of the area, based on relative numbers of mule deer observed in 28.8-ha blocks during all aerial surveys from 1976 through spring 1984 (Fig. 7.1) indicated that spatial distribution was neither uniform nor random. Rather, it followed a clumped or aggregated pattern. Both general and local aggregation, characterized by areas of relatively high deer density bordered by areas of declining density, was apparent.

Across the area as a whole, moderate to dense concentrations generally extended across broken terrain along slopes and coulees between major ridgetops and major coulee or river bottoms. Highest contiguous densities occurred in the northwestern portion of the area between Sand Creek and the Missouri River. Blocks in which deer were never or only rarely recorded were primarily in open prairie habitat along the southern and southwestern fringes, larger expanses of sagebrush-grassland along major ridges, large open coulee bottoms within a few kilometers of the Missouri River, and bottomlands along the river. These areas did not comprise yearlong habitat for mule deer and received only occasional seasonal or transitory use.

Within this general pattern, aggregated areas of high density were surrounded roughly concentrically by areas of lower, declining use. A quantitative representation of concentric distribution around high density blocks (Table 7.1) indicated that adjacent blocks were not randomly distributed among the 4 density categories ($X^2 = 164.6$, 3 df, $P < 0.0001$). Other blocks of high density were significantly over

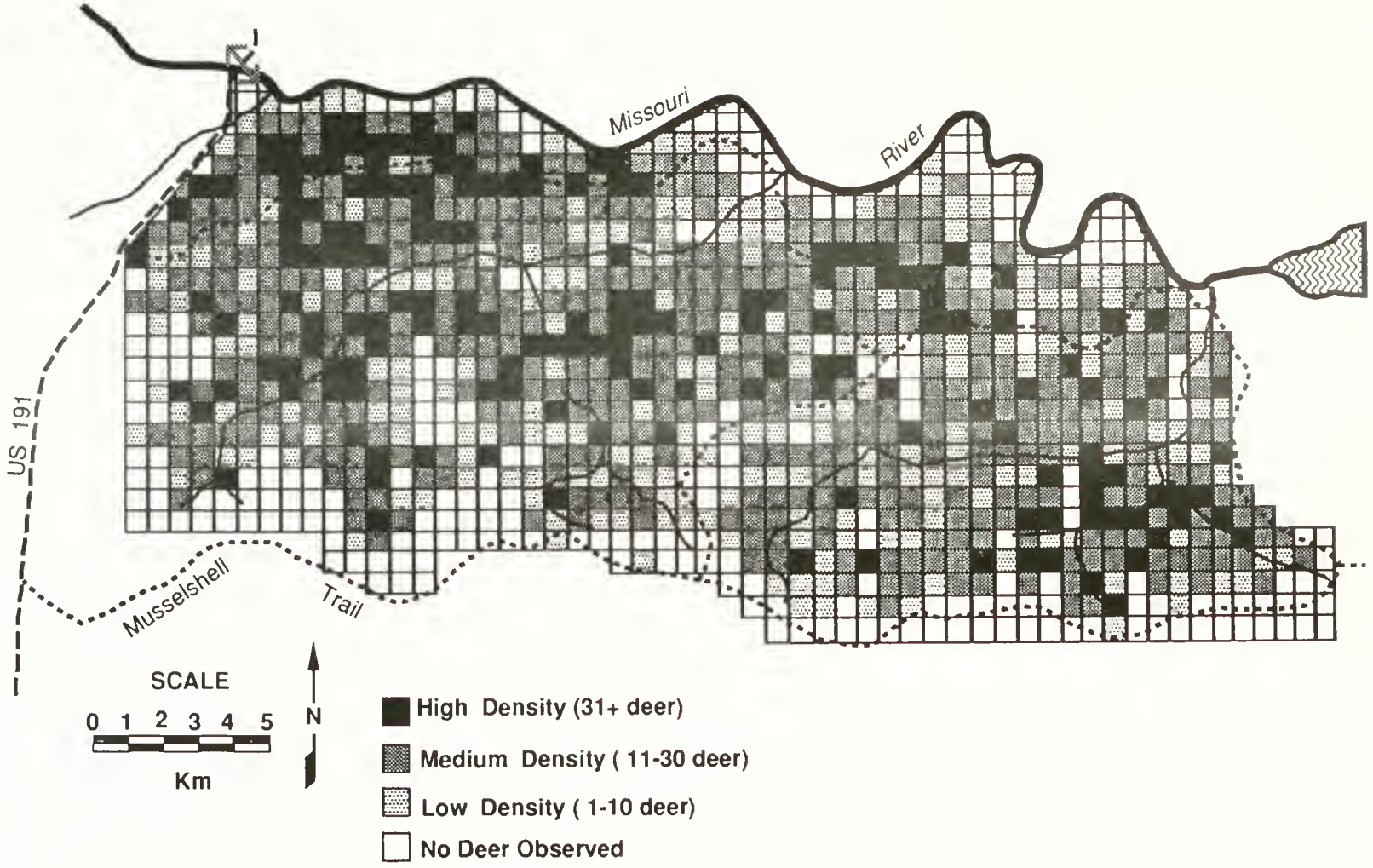


Figure 7.1. Relative density distribution (intensity of use) for mule deer as determined by data from 32 aerial surveys during 1976-1984.

Table 7.1. Relative density distribution of mule deer in the Missouri River Breaks, Montana, 1976-1984.

Block Type	Proportions of adjacent blocks that were: High Density	Medium Density	Low Density	No Deer Use
High Density	0.282	0.519	0.158	0.041
Medium Density	0.211	0.472	0.241	0.076
Low Density	0.125	0.472	0.238	0.165
No Deer Use	0.036	0.179	0.206	0.579
Overall Distribution of blocks	0.177	0.423	0.231	0.169

represented, while blocks in which deer were never observed during the aerial surveys were significantly under represented. Blocks of medium density occurred in greater than random proportion adjacent to high density blocks, while low density blocks occurred in lower than random proportion. Blocks surrounding medium, low, and zero density blocks also were not randomly distributed (X^2 = 137.7, 3 df, P < 0.0001; X^2 = 19.6, 3 df, P < 0.0001; X^2= 553.7, 3 df, P < 0.0001; respectively). In each case, blocks of the same density category were positively associated, while those 2 or 3 density categories higher or lower were negatively associated. These data together with Figure 7.1 indicate a general dispersion pattern characterized by a high degree of aggregation in and around "core" areas or habitats, and gradual rather than abrupt transitions in density distribution.

Spatial Distribution by Sex and Age

Spatial distribution by sex and age classes was quantified only during autumn when all deer were about equally visible and dispersion was not altered by years of varying winter severity. We tested by Chi-square and correlation analysis the null hypothesis that there were no differences in spatial distribution between sex and age classes. This hypothesis was rejected in all tests except for the comparison between females and fawns (Table 7.2), which, as expected, were not distributed differently. Spatial distribution of females and fawns, however, was different from that of both yearling and mature males, and yearling and mature males were also distributed differently.

Correlation analysis indicated the degree and direction of association between sex and age classes (Table 7.3).

Table 7.2. Chi-square probabilities that distribution among 28.8 ha blocks for adult females, fawns, mature males, yearling males, and total males during autumn, 1976-1983 was not significantly different.

	Fawns	Mature Males	Yearling Males	Total Males
Adult Females	X^2=250.2 P=1.000 df=445	X^2=788.9 P=0.000 df=489	X^2=720.2 P=0.000 df=493	X^2=864.4 P=0.000 df=521
Fawns		X^2=714.8 P=0.000 df=425	X^2=687.2 P=0.000 df=436	X^2=827.7 P=0.000 df=471
Mature Males			X^2=352.8 P=0.003 df=283	

Table 7.3. Spearman correlation coefficients indicating degree and direction of association in distributions among 28.8 ha blocks for adult females, fawns, mature males, yearling males, and total males during autumn, 1976-1983.

	Fawns	Mature Males	Yearling Males	Total Males
Adult Females	0.589 P=0.0001 N=446	-0.098 P=0.03 N=490	-0.040 P=0.39 N=494	-0.054 P=0.22 N=522
Fawns		-0.245 P=0.0001 df=426	-0.212 P=0.0001 df=437	-0.204 P=0.0001 df=472
Mature Males			-0.225 P=0.0001 df=284	

Females and fawns, again as expected, were significantly positively associated; though the correlation coefficient did not approach 1.00 because not all females produced or reared fawns each year. The distribution of females was significantly negatively correlated with the distribution of mature males and was also negatively correlated with yearling males, but not significantly. The negative correlation between distributions of fawns and mature males was significant as was that between fawns and yearling males. Distributions of yearling and mature males also were significantly negatively correlated with each other.

The stronger negative correlation between fawns and mature males than between females and mature males indicated that mature, productive females with fawns generally were distributed differently than mature males, whereas non-productive females often occurred in the same 28.8-ha blocks as males. The data also indicated that yearling males were more widely distributed and occurred in the same blocks as females more often than mature males.

Temporal Changes in Spatial Distribution

Comparison of Figure 7.1 with a more generalized map of density distribution of mule deer on the study area during 1960-1964 (Fig. 7.2, Mackie 1970) indicated that areas of highest and lowest densities were reversed for the 2 periods of intensive study. This difference may have been influenced by 2 major environmental changes. The first involved changes in timing of livestock grazing. The area of comparatively high mule deer density during 1960-1964 was centered around a private ranch on which cattle were grazed only during winter. In about 1970, the area was leased to other operators and thereafter heavily grazed during spring and occasionally grazed during other seasons. Winter grazing with supplemental feeding probably had little effect on the composition and abundance of spring and summer forage for deer and may have made spring growth more available. The absence of livestock in this diverse drainage-head habitat of moderate to low topographic relief may also have rendered succulent, high-quality forage more available through summer. Conversely, heavy grazing during spring over several years may have reduced the quantity and quality of summer forage and decreased quality of the area as fawn-rearing habitat.

Grazing practices along the northern and northwestern portion of the area, which held relatively low deer densities in the early 1960s and high densities in recent years, followed the opposite trend. Headquarters ranches and winter livestock grazing and feeding operations along the Missouri River were phased out during the 1970s. There, habitats adjacent to the river that had been moderately to heavily

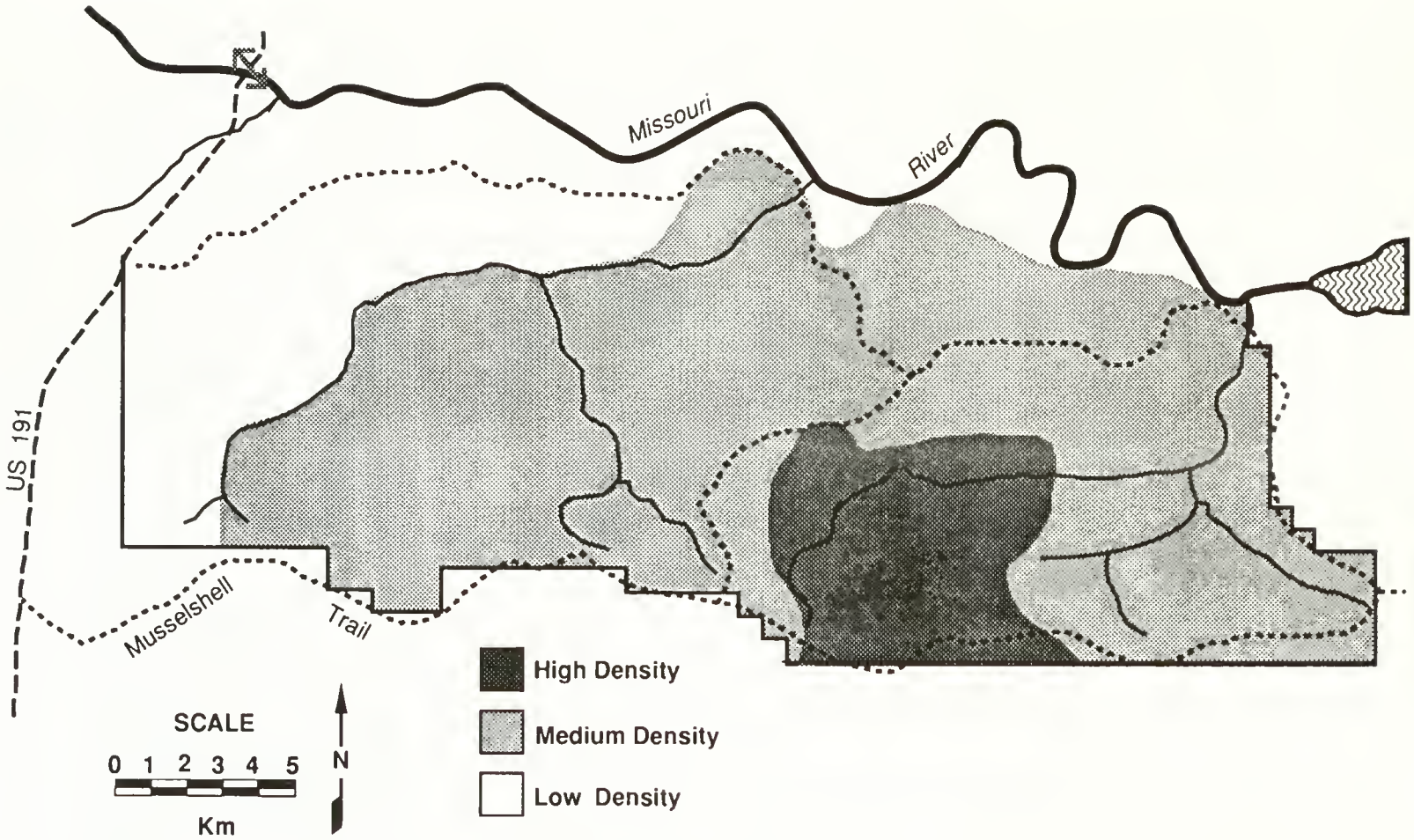


Figure 7.2. Relative density distribution of mule deer during 1960-1964 (from Mackie 1970).

grazed in spring and summer as livestock were turned onto uplands from the bottoms came to receive little or no spring grazing and only light to moderate use during summer and autumn. Thus, the quantity and quality of available summer forage probably increased progressively through time.

The second major environmental change occurred as a result of wildfire that burned approximately 315 ha of Douglas fir habitat on the northwest portion of the study area in 1961. Because areas adjacent to the burn also had low densities of deer during the 1960s, it is unlikely that displacement of deer from burned to unburned habitat was responsible for the average low deer densities in the area through 1964. It seems more likely that regrowth of shrubs and forbs improved forage conditions (Eichhorn and Watts 1984) and led to more intensive deer use after the mid-to-late 1960s. Knowles (1975) also reported disproportionately high deer use in the vicinity of burns in similar habitat on the NCRCA.

Other temporal changes or variations in spatial distribution occurred in relation to seasonal movements, winter severity, and trends in density of deer on the study area. Overall, mule deer were observed in 792 (83%) of the 953 28.8-ha blocks during the 32 full-coverage aerial surveys from 1976 through 1984. They occurred in 64%, 60%, 65%, and 53% of the blocks during summer, autumn, winter, and spring, respectively. However, because individuals were less observable and fewer total deer were seen during summer and autumn than during winter and spring, these data were adjusted based on the number of different blocks/deer observed. Relative to the number observed per season, deer were most widely dispersed among blocks during summer, followed by autumn and winter-spring. This was also expected on the basis of increasing group sizes that indicated increasing aggregation from summer through spring.

As deer numbers declined across the area during the early 1970s, a disproportionately large decline occurred in counts within subdivisions along the southern fringes of the area adjacent to the prairie. Similarly, population growth during the late 1970s and early 1980s was marked by a disproportionately greater increase in fringe areas, especially in the southcentral and southwest. Regardless of the manner of data collection, deer moved from areas of low relief near the prairie to areas of steeper terrain near the river during severe winters with deep snow cover. That distributional change was also documented by movements of marked and radio-collared deer during 1976-1984.

More specific data on relationships between changes in deer numbers and spatial distribution were obtained during the

period of population increase from 1976 to 1983. Average adult female density across the study area increased from 1.08/km^2 during 1976-1978 to 2.66/km^2 during 1981-1983. At low densities, the contiguous blocks occupied by females (Fig. 7.3) were equivalent to the major "core areas" (Fig. 7.1). A few individual females who's distribution was not plotted in Figure 7.3 occurred in scattered, isolated blocks. Relative density distributions of females at low and high densities (Table 7.4) indicated that densities in the "core blocks", occupied throughout the period, did not increase as total number of deer increased. Instead, there was increased occupancy of blocks immediately adjacent to "core" blocks and in areas that were unoccupied during the population low. Blocks immediately adjacent to "core blocks" ultimately filled to about the same relative density as the "core". Thus, neither increases nor decreases in total deer numbers occurred equally across the area. Populations in "core blocks" remained relatively stable, while most of the changes occurred in adjacent areas. During population increases, blocks adjacent to "core blocks" were occupied by yearlings recruited from the "core blocks". Occupancy of more distant, previously unoccupied habitat may result from presaturation dispersal of yearling females from "core areas" (Lidicker 1978).

We do not imply that numbers of deer within broad "core areas" did not increase with population size. Most yearling females used the same general home range area as their mothers. Thus, absolute density within the broad "core" increased with population size. However, density in small "core blocks" did not increase because mother and daughter did not use the same sites at the same time during summer and early autumn, and the younger females increasingly used blocks immediately adjacent to those used most intensively by established matriarchs.

Social Organization and Distribution

Little information has been published on the social organization of mule deer. Geist (1981) discussed the behavior, but not specifically the social organization of Rocky Mountain mule deer (*O. h. hemionus*). He stated (Geist 1981): "Unfortunately, there is no study to indicate whether black-tailed deer and mule deer normally live in groups that are closely related genetically." Most existing information on social organization (Dasmann and Taber 1956, Miller 1970, and Miller 1974) relates to Columbian black-tailed deer (*O. h. columbianus*). Considerably more detailed information is available on the social organization of white-tailed deer (Hawkins and Klimstra 1970, Hirth 1977, Nelson and Mech 1981, and Ozoga et al. 1982a).

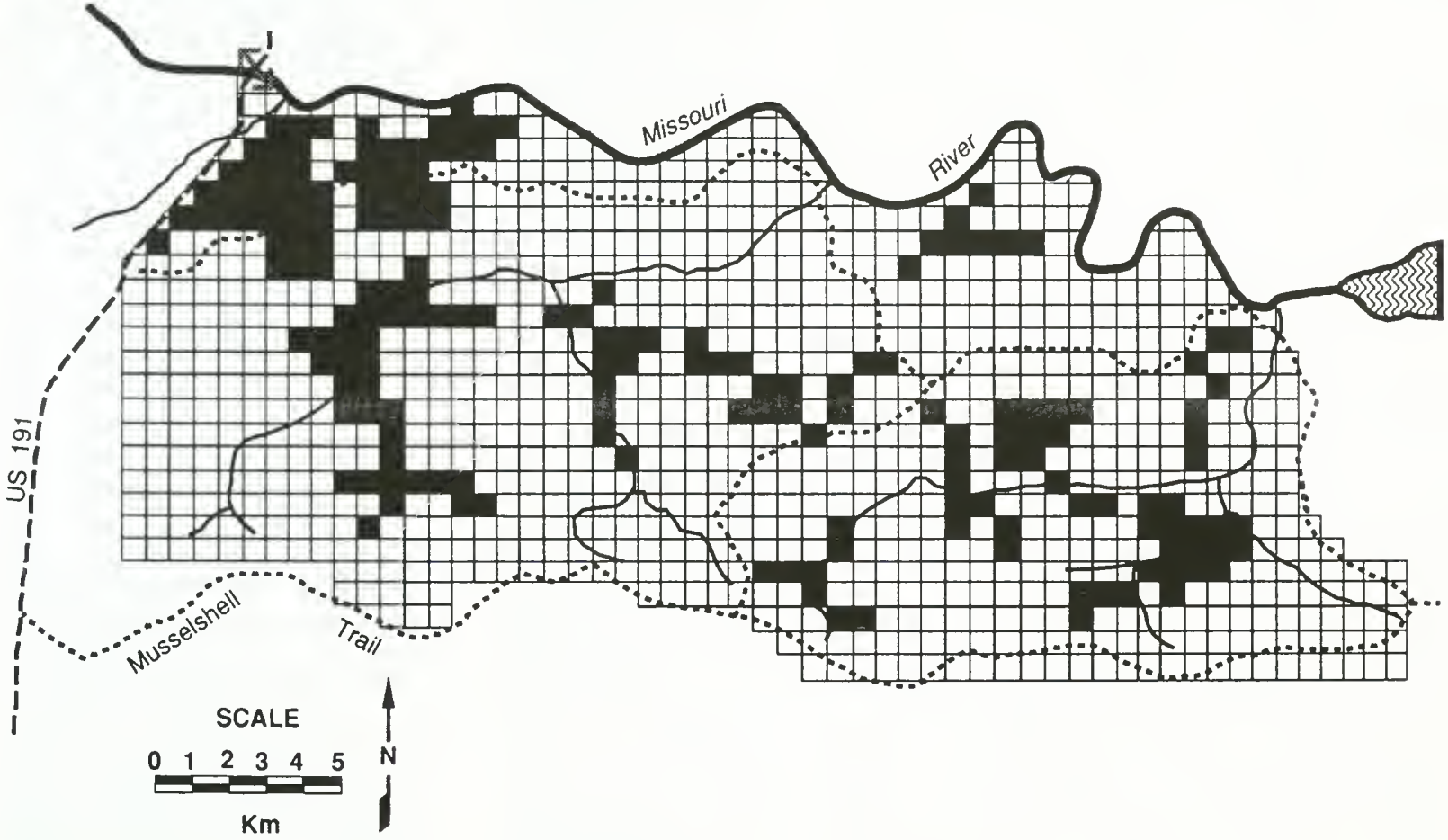


Figure 7.3. Contiguous blocks occupied by mule deer females during low population numbers, 1976-1978.

Table 7.4. Relative distribution of female mule deer densities at low (1976-1978) and high (1981-1983) density populations, Missouri River Breaks, Montana.

Type of area at low densities	Size of area (Km^2)	Female Density 1976-1978 (No./Km^2)	Female Density 1981-1983 (No./Km^2)
Female core blocks	52.1	4.17	3.86
Scattered female blocks	15.0	4.48	3.86
Blocks within 0.8 km of female core blocks	79.2	0.15	3.40
Blocks used by deer at high densities	81.7	0.0	2.51
Blocks never used by deer	4.6	0.0	0.0
Entire Study Area	274.3	1.08	2.66

We were able to collect information that increases the knowledge about social organization of Rocky Mountain mule deer and its relationship to population dynamics.

Additionally, by use of marked deer, we were able to determine the social relationships among maternally related deer.

Group Size and Composition

Group size statistics were computed for 4 categories of deer: total deer, adults only, adult females only, and adult males only. Group composition data were tabulated for 3 sex-age categories: yearling males, mature males, and adult females. Within each of those categories, 5 types of social groups were delineated. Using yearling males as an example, the social groups were: 1) solitary yearling male, 2) yearling male(s) with mature male(s), 3) multiple yearling males, 4) yearling male(s) with adult female(s), and 5) yearling male(s) in a mixed group containing at least 1 each of yearling male, mature male, and adult female.

Mean group size for total deer, adults, and females increased from the fawning period through March (Table 7.5, Fig. 7.4). Data from mature female groups (Fig. 7.4)

Table 7.5. Mule deer group sizes during aerial surveys in the Missouri River Breaks, September 1976 through April 1984.

Time	Group: All Deer	Adults only	Adult Females only	Adult Males only
July	1.59±0.04[a]A[b] (1-7)[c] 2659[d] 1626	1.29±0.03A (1-6) 1163	1.08±0.02A (1-4) 548	1.53±0.07A (1-6)
Sept.-Oct.	2.4±0.07B (1-11) 1400 1382	1.61±0.05B (1-8) 1009	1.46±0.05B (1-6) 480	1.55±0.08A (1-7)
Late Nov.-Early Dec. (Rut)	3.04±0.25C (1-14) 190 186	1.85±0.15C (1-8) 161	1.53±0.15B (1-8) 88	1.10±0.07B (1-3)
Late Dec. - Early Jan.	3.30±0.11C (1-16) 1645 1593	2.05±0.07C (1-10) 1356	1.92±0.07C (1-10) 465	1.42±0.07A (1-6)
Mar.-Apr.	4.52±0.18D (1-20) 1061 1052	3.01±0.13D (1-13)		

[a] $\bar{X}$ ± 95% CI
[b] Means in columns followed by different letter are different, $P<0.05$.
[c] Range of group sizes
[d] Number of groups

indicated that group size then declined through April and May to annual lows during June and July. The number of females per group was lowest during July (and probably late June) when an average 85% of all adult females did not occur in the same group with another female. Number of males per group peaked during summer and early autumn, but observations of marked males suggested that group size for mature males may have reached another high during mid-winter through spring. For a small sample of 59 observations of marked mature males during mid-January through mid-May, where the entire group sex-age composition was known, there were the fewest solitary mature males and greatest percentage of mature males with other mature males of any recorded period (Table 7.6). The smallest group size for males was during the rut when 82% of males did not occur in a group with other males.

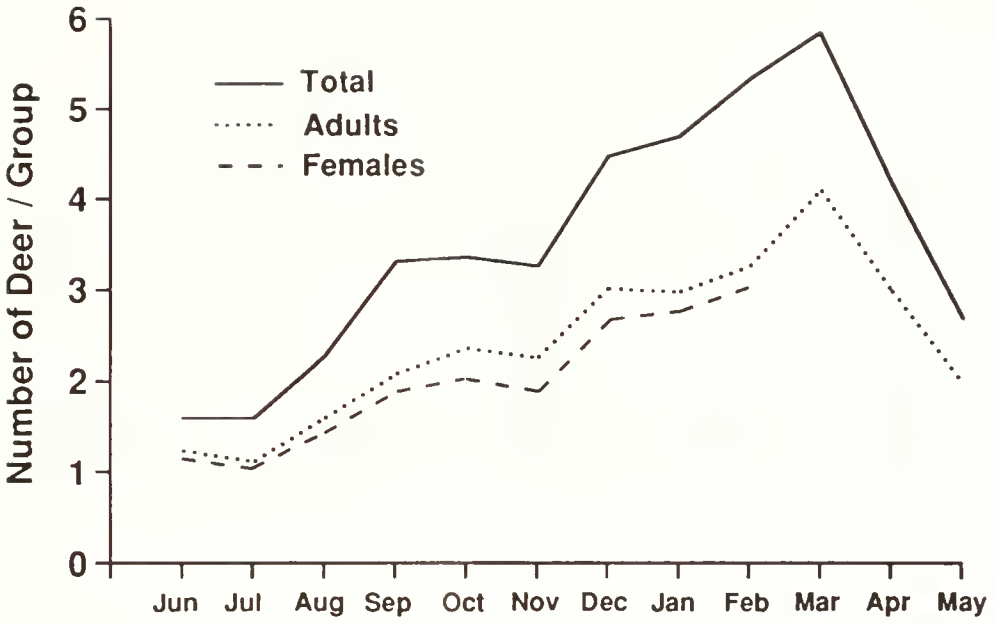


Figure 7.4. Group size by month for 37 radio-collared 2-year-old and older females.

During summer and early autumn, yearling males were almost equally distributed among all types of social groups (Table 7.6). However, during July, only 10 yearling males (2.4%) were seen with females that had fawns. Information from marked deer indicated that most of the females observed in association with yearling males during summer were either yearling females or non-productive mature females.

The percentage of solitary yearling males declined from July through the remainder of the biological year as yearling males increasingly associated with females. The greatest degree of association between yearling males and mature males occurred during summer and declined thereafter. The lowest association with other males occurred during the rut. A small sample of 63 observations of marked yearling males indicated that most (74.6%) were associated with females during mid-January to mid-May (Table 7.6, Fig. 7.5).

During summer and early autumn, mature males were typically solitary or grouped with other males (Table 7.6). Very few (<13%) were associated with females during summer or early autumn. During the rut, no mature males were observed with any other male, except when both were competing for the same female. Eighty percent of mature males observed during the rut were in groups containing females, the other 20% were solitary. During early winter, as rutting behavior

Table 7.6. Percentage of yearling males, mature males, and adult females in various social groups by time period, Missouri River Breaks, 1976-1984.

Social Group	TIME				
	July	Sept.-Oct.	Late Nov.-Early Dec.	Late Dec.-Early Jan.	Late Jan.-Mid May
Yearling Males					
Solitary	37.6	27.1	26.8	19.3	12.7
With Mature Males	17.4	16.5	0.0	10.8	7.9
With Other Yearling Males	25.8	29.5	7.1	12.8	4.8
With Adult Females	17.8	21.5	58.9	47.2	71.4
With Mixed Males & Females	1.4	5.4	7.1	9.8	3.2
N	426	424	56	398	63
Mature Males					
Solitary	32.8	33.3	19.5	27.7	15.3
With Yearling Males	22.9	20.2	0.0	16.7	10.2
With Other Mature Males	36.6	34.0	0.0	19.3	55.9
With Adult Females	5.8	8.4	68.3	22.7	15.3
With Mixed Males & Females	1.9	4.1	12.2	13.6	3.4
N	415	321	41	264	59
Adult Females					
Solitary or with Fawns Only	81.2	41.9	24.3	22.9	
With Other Females (and Fawns)	10.9	46.5	40.9	56.1	
With Yearling Males	5.5	8.1	19.4	13.0	
With Mature Males	1.9	1.9	12.1	5.2	
With Mixed Males & Females	0.6	1.7	3.2	2.8	
N	1260	1474	247	2601	

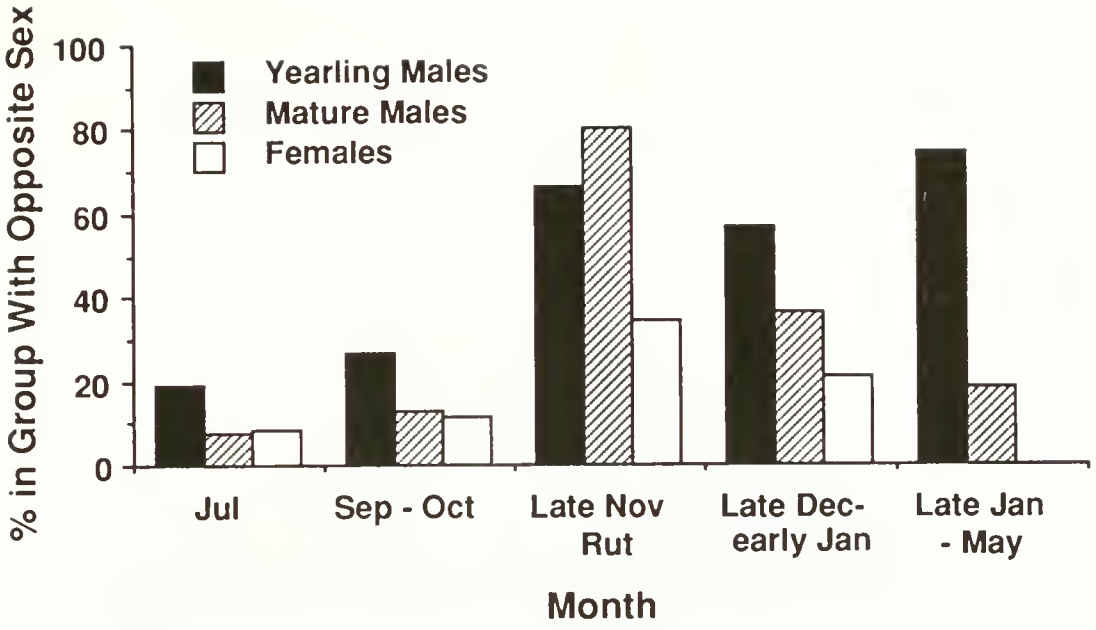


Figure 7.5. Percent yearling and mature males in groups containing females and percent females in groups containing males during various time periods.

diminished, mature males were well distributed among all 5 types of groups. From mid-January through mid-May, 55.9% occurred in groups containing only mature males.

Over 80% of all adult females observed were solitary or associated only with new fawns during July. This percentage varied among years, depending upon the percentages of yearling and non-producing mature females in the population. Most females that were not solitary during July did not have fawns. Only about 8% of mature females were observed with males during July (Table 7.6, Fig. 7.5). Yearling females, however, were grouped with other adult deer in 57% of 170 observations of 25 marked yearling females during June-August. By early autumn, females were about equally as commonly observed as solitary adults accompanied only by fawns or grouped with other females and fawns. Females were most commonly grouped with other females and fawns during and after the rut. At the peak of rut, 35% of all females observed were in groups containing a male (Fig. 7.5). The percentage of females observed with males declined thereafter. Of all males associated with mature females, the percentage that was mature males reached a peak during November and December (Fig. 7.6). Most males observed with females at other times of the year were yearlings.

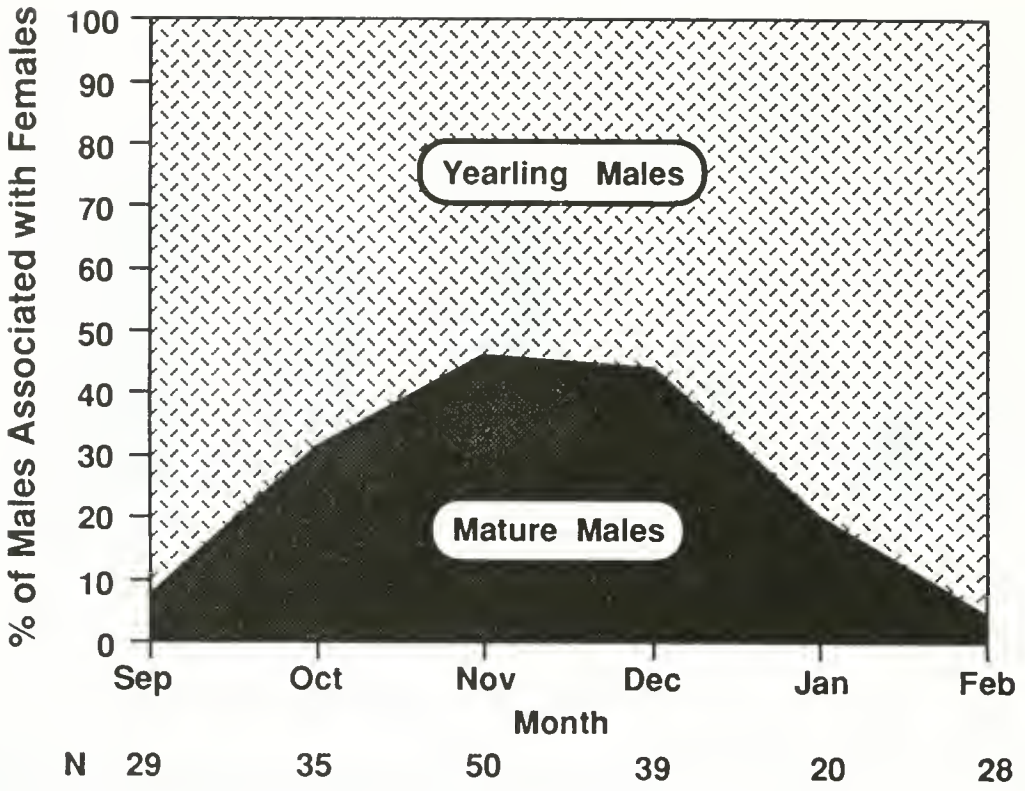


Figure 7.6. Age of males associated with radio-collared 2-year-old and older females during September through February.

Factors Influencing Group Size and Composition

The increase in group size from June-July through March despite a decline in total deer density through the period indicated that seasonal change in group size resulted from changing sociability and habitat use rather than changes in deer density during the year.

To determine whether seasonal group size changed from year-to-year as density of deer changed, correlations between annual deer numbers on the study area (density) and group size during autumn and early winter each year 1976-1985 were computed. The null hypothesis that group size did not increase as deer density increased was not rejected in any case. Correlation coefficients between deer numbers during autumn and group size were: total group size, r=-0.242, n=10; adult group size, r=-0.067, n=10; and female group size, r = -0.102, n=10 (all P's > 0.05). Coefficients between deer numbers during early winter and group size were: total group size, r=-0.263, n=9; adult group size, r=-0.121, n=9; and

female group size, r=-0.180, n=9 (all P's > 0.05). Deer numbers were 3.15 times higher at the high than the low, so the available range of densities should have been sufficient to show differences if they occurred. Although statistically non-significant, the negative correlation coefficients may indicate a tendency toward smaller group size as density increased.

General observations suggested that mature females were socially oriented towards their fawn(s) first, and exhibited minimal relations with other adult deer. However, as the biological year progressed from fawning, females increasingly associated with other females, especially during years of poor fawn survival. This suggested that female group size was related to fawn survival. A test of that hypothesis with correlation analysis indicated a strong negative relationship (Figs. 7.7 and 7.8) between the number of females per group and fawn:100 female ratio in the population during autumn ($r=-0.907$, $P<0.01$, $n=14$). A similar relationship was indicated with respect to numbers of fawns:100 females in the population during early winter ($r=-0.920$, $P<0.01$, $n=15$). Data for autumn 1985 were not included in the analysis; that data point did not fit the linear regression line, probably because most fawn mortality had occurred by mid-summer such that females had a longer than usual time to reassociate prior to the autumn survey. These correlations indicated that the higher fawn production and survival through early winter, the less likely that females were associated with other females. Group size increased as fawn survival declined both within and between years.

The same data displayed in a different manner (Fig. 7.9) led to additional conclusions. During early autumn, the largest decrease in fawn:female ratio occurred between single females and groups of 2 females. The degree of decline between these as compared to the decline between other sized groups indicated that the second female in the group was the most likely of all additional females to not have a fawn. Data from marked deer verified this and indicated that the second female in the group (first one added in autumn) was most likely an unproductive yearling daughter.

For the early winter period, the change in fawn:female ratio was about the same from 2 to 3 females/group as it was from 1 to 2 females/group. Again, data from marked deer indicated that by early winter, the third female added to a group was most likely to be either a second yearling daughter that had not rejoined the family group by early autumn or an unproductive 2-year-old daughter. Little difference in fawn:female ratios occurred among female group sizes 3, 4, 5, and 6 during early winter, indicating that the fourth, fifth, and sixth females added to a group were about equally likely

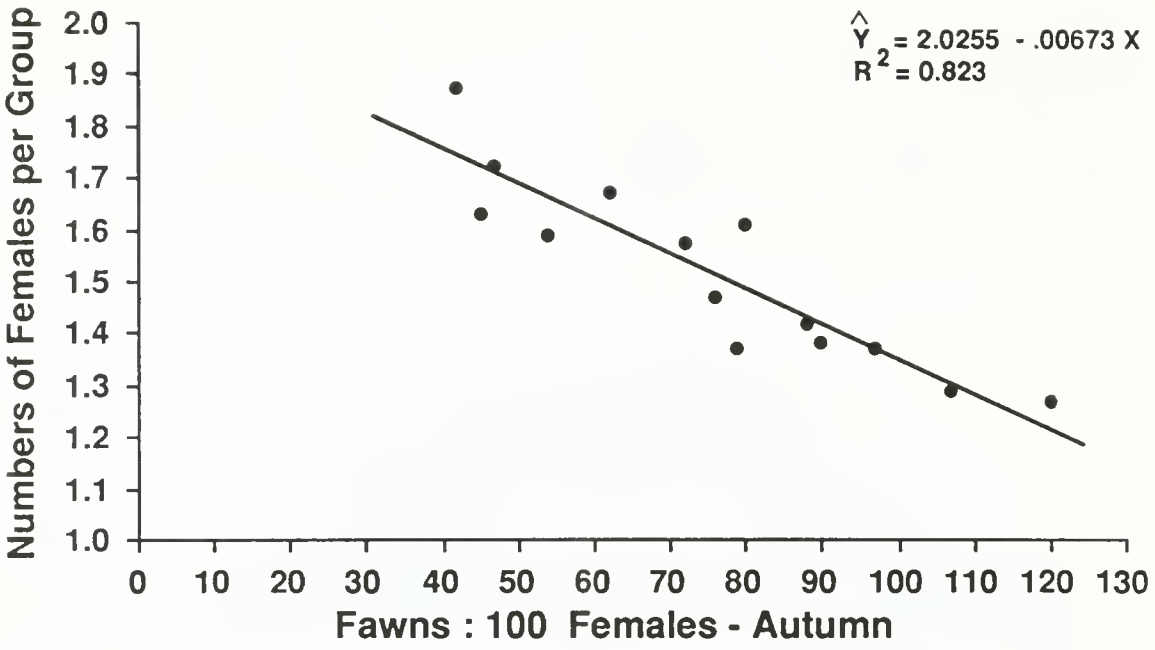


Figure 7.7. Relationship between number of females per group and the fawn:100 female ratio during autumn

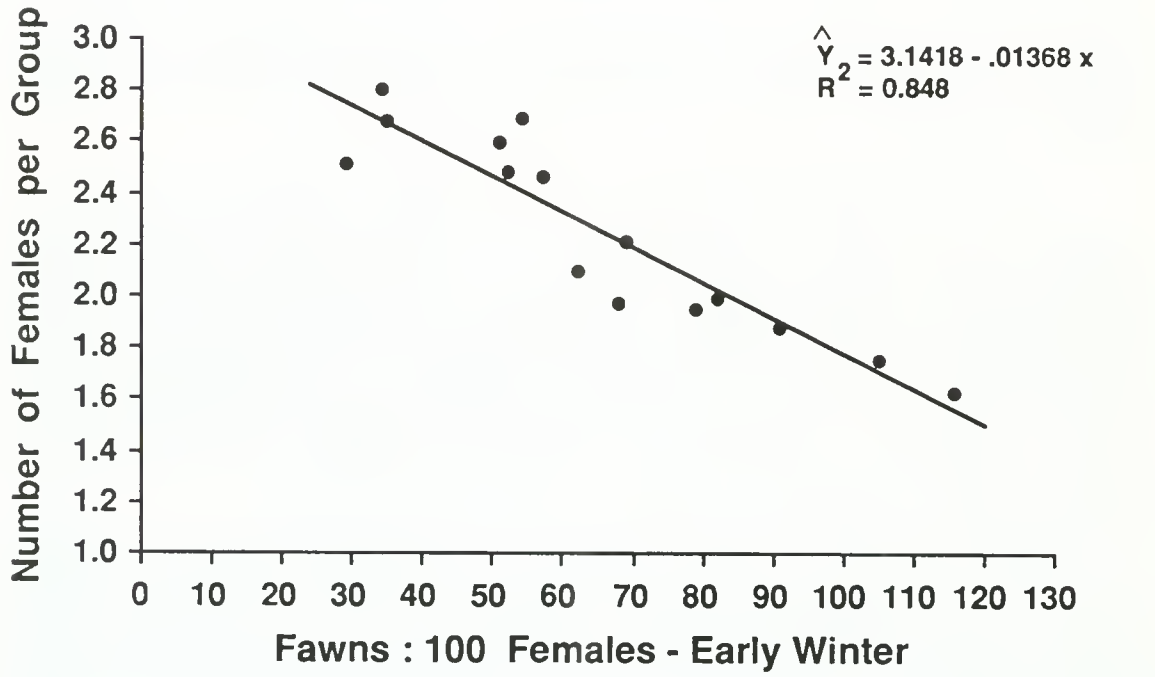


Figure 7.8. Relationship between the number of females per group and the fawn:100 female ratio during early winter.

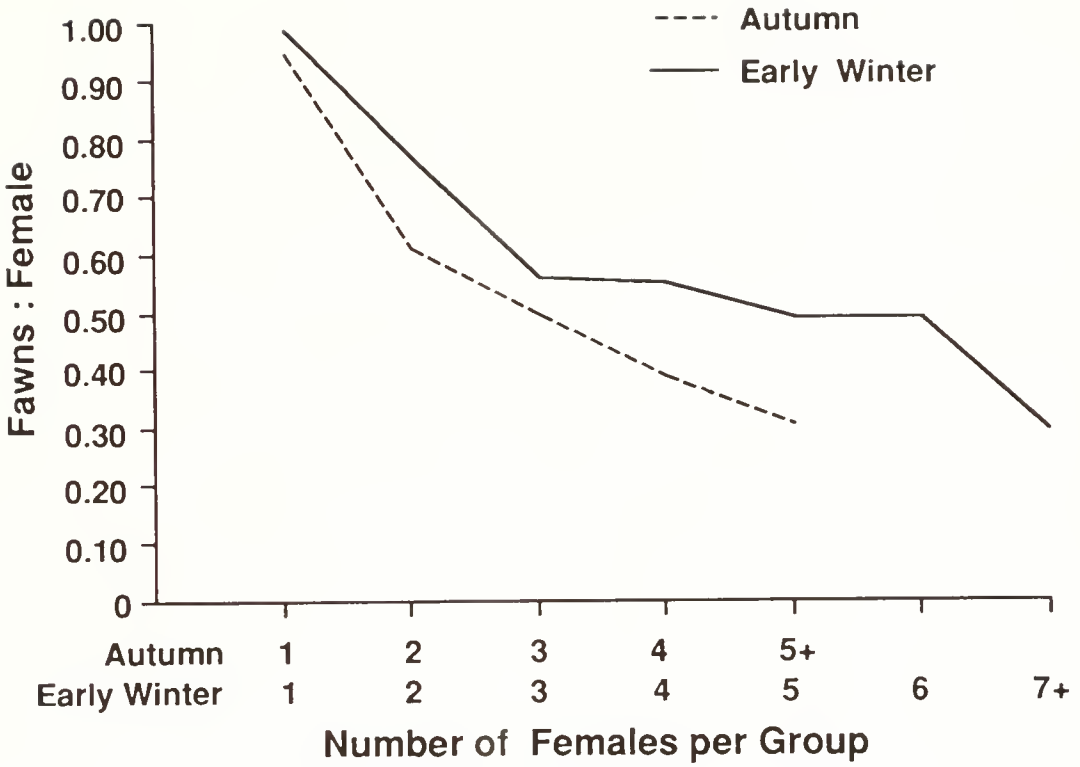


Figure 7.9. Per capita fawn production in relation to female group size, 1976-1984.

to have or not have a fawn. Some of those females were productive older daughters. Also, beyond the fourth generation (3 adult generations), daughters were most likely to establish their own matrilineal group.

A total of 74% of all adult females observed during autumn occurred in groups of 1 or 2 adult females. Forty-three percent of all females observed did not occur in groups with other females and 31% occurred in a group of only 2 females. During early winter, approximately equal numbers of adult females were in groups containing 1, 2, or 3 adult females; those 3 group sizes accounted for 67% of all females observed.

The percentages of all deer, of all sex and age classes, that were observed in each group size are shown in Figure 7.10. From autumn through spring, more deer occurred in groups of 3 than any other group size. Averaged for all 3 seasons, 20.0% of all deer observed were in groups of 3 and 15.7% were in groups of 4. Group sizes of 3 and 4 may be most observed because the most common social group, a female or 2 females and their fawns, are usually a group of 3 or 4 deer.

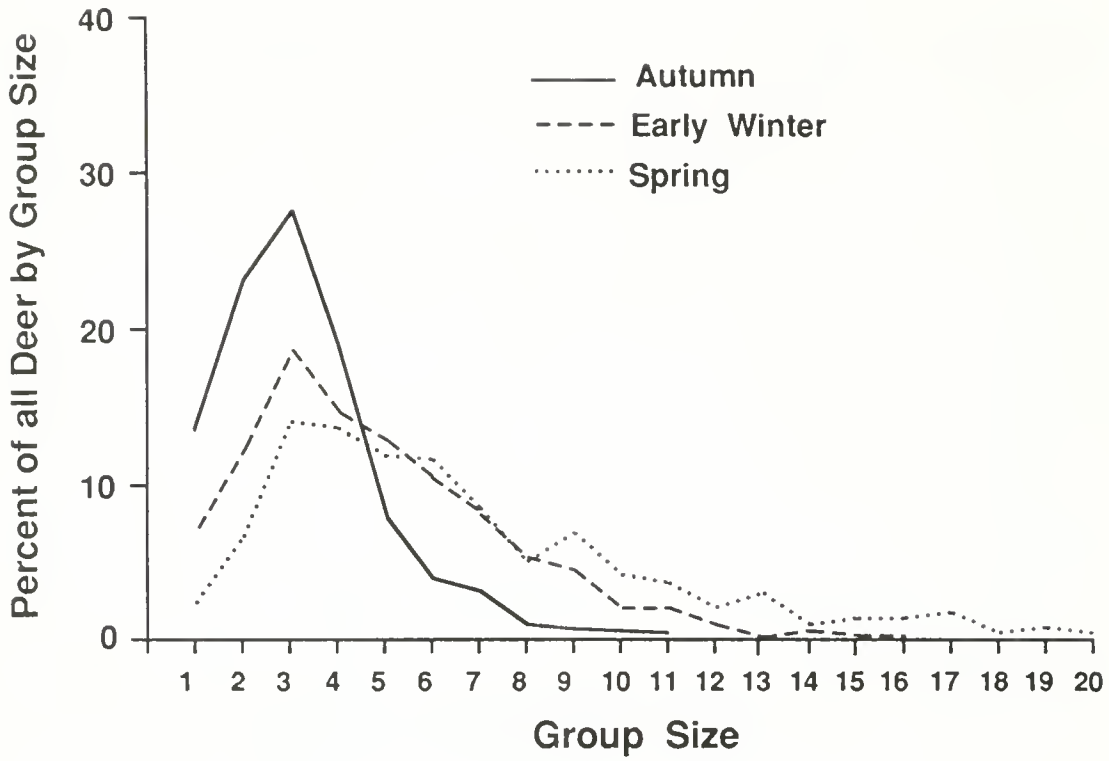


Figure 7.10. Percent of all deer occurring in various sized groups during autumn, early winter, and spring.

Associations of Genetically Related Individuals

Mother-Son and Sister-Brother Relationships

Very few mother-son or sister-brother combinations remained associated with each other after 1 year of age. At 12-14 months of age, 40 (70%) of 57 marked yearling males monitored, dispersed from their natal home range and 29 (51%) of those left the study area (Table 7.7). This meant that after 14 months of age (before their first breeding season), 70% of all males were no longer associated with their mother or sisters. Opportunity for the remaining males to associate or breed with relatives was also limited.

Among 17 yearling males that had not left their natal home range by late August, at least 4 had no opportunity to breed with maternally related females. Three of these were shot before the rut, and 1 dispersed 5 km away prior to the rut and did not return until afterward. Five others used areas that included their natal range during their first breeding season. Of these, 1 used an area that included its

Table 7.7. Dispersal rates of yearling mule deer, Missouri River Breaks, Montana, 1976-1985.

	Males			Females		
Birth Year	N	% Dispersal from Natal Area	% Dispersal from Population	N	% Dispersal from Natal Area	% Dispersal from Population
1976-78	9	100	78	10	10	10
1979	11	64	46	11	27	27
1980	11	64	46	15	27	27
1981	7	71	57	10	10	0
1982	11	55	27	11	0	0
1983	4	100	75			
1985	4	50	50	1	0	0
Total	57	70	51	58	16	14

natal range through the second breeding season and 2 used the natal range through 4 breeding seasons. Radio failure or harvest by hunters precluded gathering further information on these 5.

Potential for breeding with maternally-related females was not determined for the remaining 8. Six of these were last observed prior to the rut and 1 during the rut when we ceased receiving signals from their radio transmitters. Ultimate fates of these 7 could have included: dispersal beyond search range, shot during the hunting season and not reported, or remained on the area undetected. Another was shot during November, but we did not know if it was prior to or during the rut.

Five males remaining within their natal ranges had marked mothers and/or sisters. Male 3379 remained within his mother's (3578) home range (Fig. 7.11) throughout 22 months that his radio collar functioned. He was never observed with his mother after 1 year of age (16 observations) except at 13 months of age on 9 July 1980, when she was chasing him. No male with a fawn-type radio-collar or ear tags was ever observed with female 3578 during the remaining 25 months she was alive.

Male 2581 and his twin sister 2381 were the offspring of marked female 2481. Brother and sister were together 4 of 6 times they were observed as yearlings. On 14 October they were observed together with their mother and her current fawn. What relationships, if any, that would have occurred during the rut were not determined because the sister was shot by hunters on 31 October and the mother on 9 November.

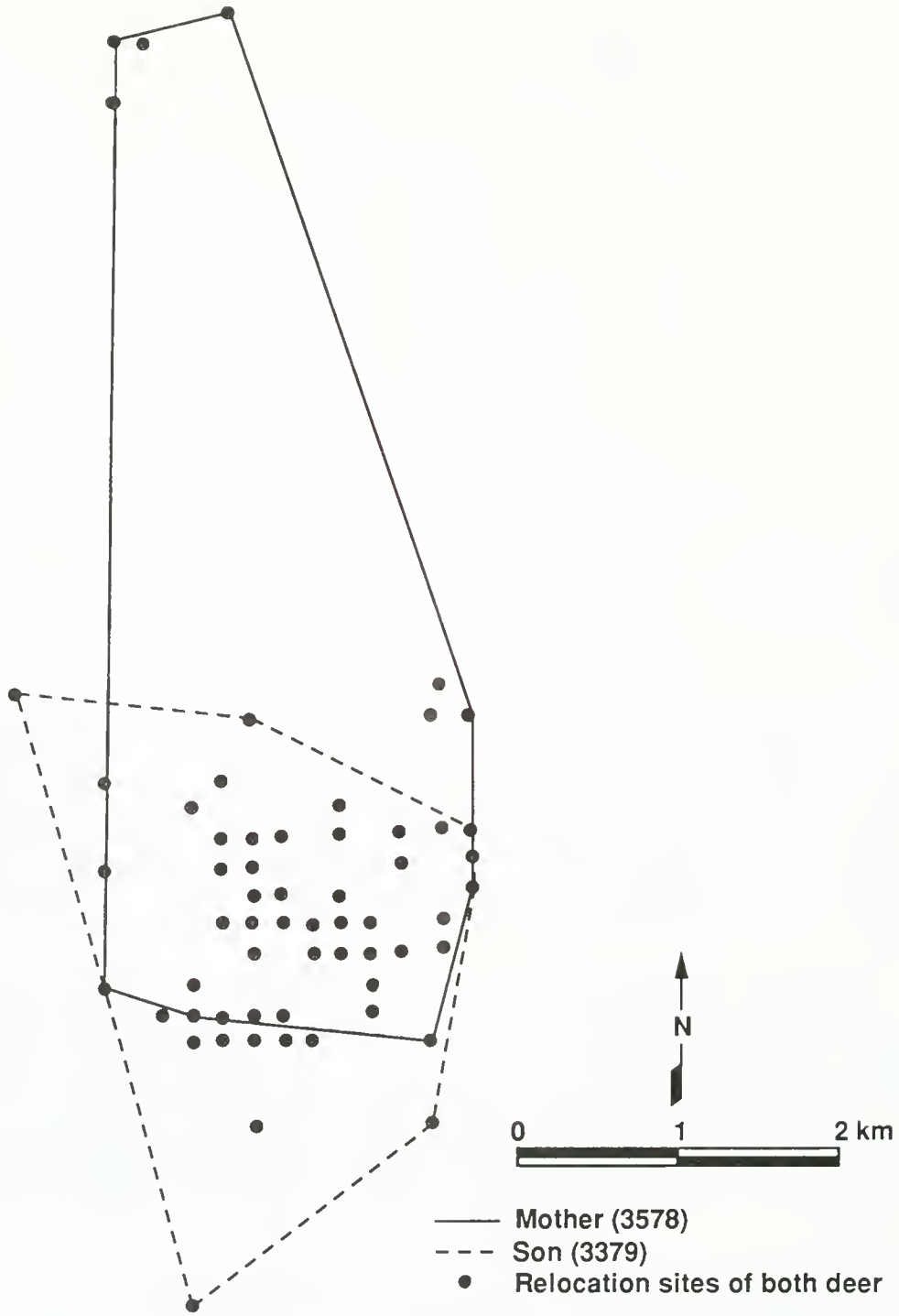


Figure 7.11. Home range boundaries and relocation sites for female 3578 and her son 3379 over a 22 month period.

Observations were made on all members of a set of triplets, 2 females (3480 and 3580) and a male (3680), through 2 years of age. After 1 year, the male was with either of the sisters during only 2 of 22 observations; both were after the rut in late January and mid-April. Male 3680 was not reobserved after that time.

After male 3581 and his sister 3681 reached 1-year-old, they were observed together during only 2 of 9 observations. This male was last observed alone during the rut on 26 November.

Male 2480 dispersed approximately 7 km from his natal home range on 3 June, but returned on 3 July. He was then seen with his sister 2580 during all 5 observations until shot on 3 November prior to the rut.

Relationships of Brothers

The available information indicated that brothers did not commonly associate with each other beyond 1 year of age. Brothers 2880 and 2980 were observed together during only 1 of 10 observations after dispersal began. On 29 May 1981, they were 1.5 km apart, but within their natal home range. By 3 June, they were about 3 km apart when both were located 7-10 km northwest of their natal range. On 4 June, both were back within the natal range, but about 0.5 km apart, and on 5 June, they were together, within their natal range. By 10 June, they had dispersed 30 and 40 km to the east where they remained apart until November, when 1 was shot and the radio-collar of the other ceased to function.

Brothers 0981 and 1081 remained together for about 2 weeks after dispersing approximately 9.5 km northeast from their natal home range. Because both wore only neckbands, they could not be reobserved at will. Male 1081 was observed alone on 16 July; 0981 was not observed at or after that time and presumably left the study area. Male 1081 was observed periodically for about 1 year within the original dispersal area where his collar was found 4 years later.

Brothers 4079 and 4179, sons of female 1577, wore non-functioning radio-collars at the time of dispersal. Although their ultimate fates are not known, they dispersed on different days and presumably did not remain together.

Relationships of Mothers and Daughters

Most mother-daughter combinations remained socially associated except during parturition and the fawn-rearing period, though degree of association declined with age when both recruited fawns. Eighty-four percent of marked yearling

females remained in the area of their natal home range (Table 7.7). Most, however, did not have marked mothers, so future relationships were not determined. The following are 6 case histories illustrating relationships between marked mothers and daughter(s).

(1) Female 1277 and her twin female fawns, 1077 and 1177, were captured and marked in February 1977. The adult female was equipped with a radio collar and both fawns marked with neckbands. From breakup of the family unit about 1 June until 14 October, 1277 was observed 6 times, never with either daughter. She was observed with a new fawn during June and July, but was not accompanied by a fawn when observed after July. Her yearling daughters were observed together on 28 May, 17 June, and 20 June. Thereafter, neither was seen until 14 October, when one (1177) was with the mother. On 27 October, the other (1077) was with the mother, but sibling 1177 was not observed. On 3 November, neither yearling accompanied 1277, but they were with her by 11 November. From then through 9 May 1978, the 3 were together in 12 of 13 observations. Daughter 1177 may have been hidden by dense timber on the 1 occasion she was not observed in the group.

From 2 June 1978 until 9 October 1978, 1277 was observed 11 times, never with either 2 year-old daughter. The 2-year-old daughters were not reobserved until 9 October, when all 3 deer were together. None of the 3 females were observed with fawns during summer, but it appeared that 1177 was followed by a fawn on 9 October. From that time through 21 April 1979, the 3 were together a minimum of 10 of 13 times they were observed. However, dense timber may have prevented observation of all deer in the group on 2 of the 3 occasions they were not all observed together. The radio-collar on 1277 failed after May 1979, and all of these deer were observed infrequently after that time.

From 28 May 1979 through 29 November 1979 (after which 1177 was never reobserved), the sisters were not together any of the 5 times that 1177 was observed. Both 3-year-old females were accompanied by twin fawns throughout the period. Neither matriarch 1277, nor 1077 was reobserved until 31 December 1979; they were first observed together on 16 February 1980. They were observed together only 2 of the 8 times that either was observed during 31 December 1979 through 23 April 1980. Both females recruited twin fawns that biological year.

During the next biological year, when 1277 was 11-years-old, and 1077 was 4-years-old, they were observed a total of 11 times, and only once (16 March 1981) were together. Both recruited twin fawns.

Thereafter, they were observed only once, on 21 September 1981, when they were together in a group of 6 adult females and 3 fawns. The matriarch, 1277, was shot by hunters on 26 October 1981. Daughter 1077 continued to used the same home range (Fig. 7.12) through 14 March 1983, after which she was never reobserved.

This matriarch and daughters continued to use the same home range (though not at the same place and time, during fawn rearing periods) as long as all were alive. The mother, and daughter (1077) that remained alive the longest, used the same home range until the mothers death at age 12-1/2; the daughter was 5-1/2-years-old. After regrouping in autumn, mother and daughter were in the same group an average of 88% of the time until the daughter reached age 3 years. During the next 2 years, when both mother and daughter recruited twins, they were observed in the same group only 3 of 19 times. During the fourth year, they regrouped early, and the indications were that at least 1 did not have fawns. Although the boundaries of their home ranges as adults were nearly the same (Fig. 7.12), they only rarely occurred in the same group when both recruited fawns. There were 2 areas used by the matriarch during the fawn-rearing period in which the daughter was never observed during June through August after she was 1-year-old (Fig. 7.12).

(2) Female 0376 and her daughter 1680 were observed from the time 1680 was 6 months old until 44 months old. Female 0376 was a minimum of 6-1/2-years-old at the time 1680 was radio-collared. Observations on this relationship ceased on 10 February 1983 when 0376 lost her collar, but the presence of 0376 through at least 14 March 1983 could be verified because she retained a matted band of hair around her neck.

After the initial breaking of the maternal bond, when 1680 was one year old, mother and daughter were not observed together until 2 September. During the remainder of that biological year, the mother, her new fawn, and daughter 1680 were together in 20 (95%) of 21 observations.

During the next biological year, both 0376 and 1680 recruited fawns and were not observed in the same group until 3 November. For the rest of that biological year they were in the same group 12 of 13 times. Both 0376 and 1680 recruited fawns during the following biological year and were not observed together until 14 December. From then until 0376 lost her collar, mother and daughter were together in 5 of 7 observations.

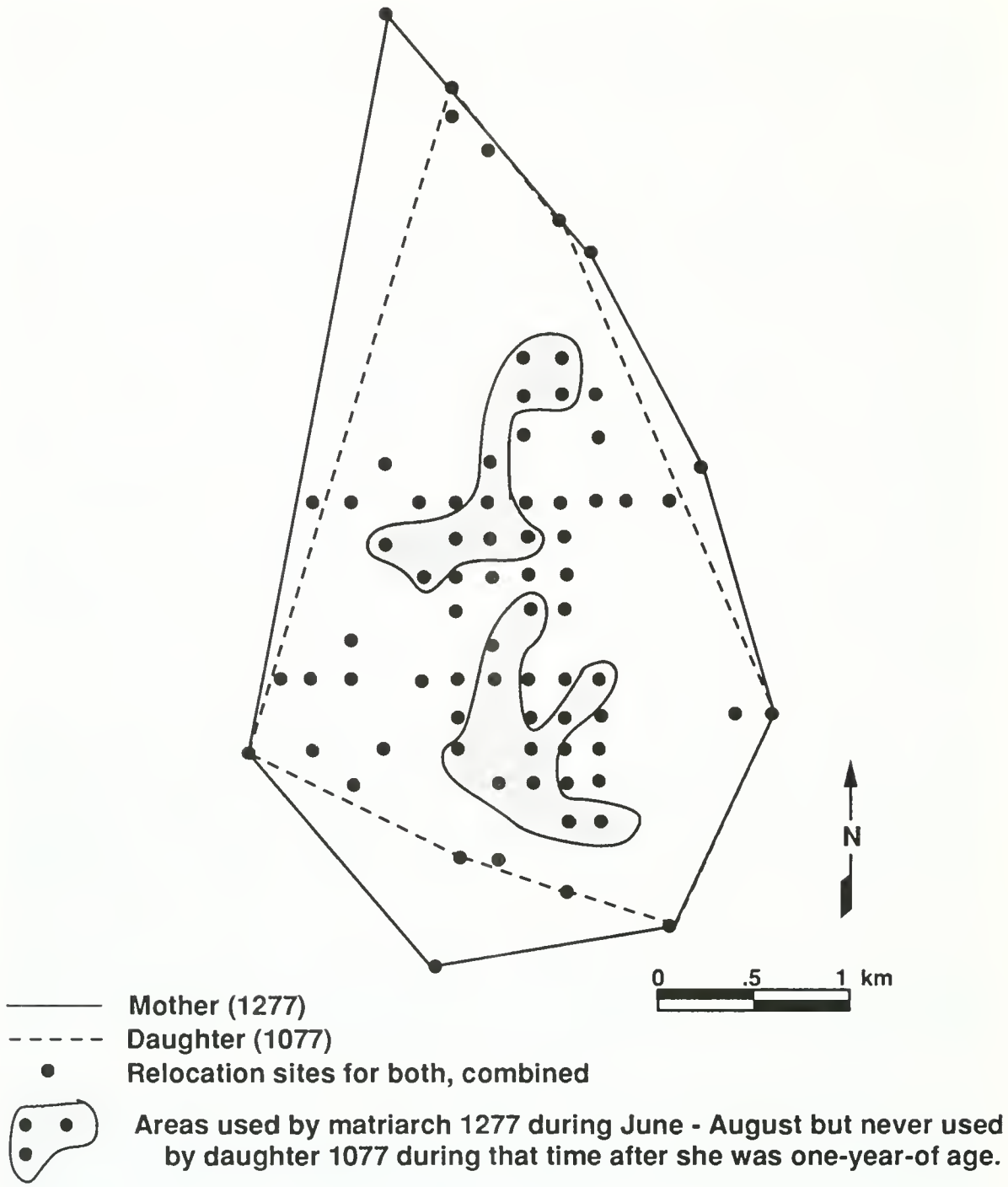

N
0 .5 1 km
Mother (1277)
Daughter (1077)
Relocation sites for both, combined
Areas used by matriarch 1277 during June - August but never used by daughter 1077 during that time after she was one-year-of age.

Figure 7.12. Home range boundaries and relocation sites for female 1277 and her daughter 1077, including areas used exclusively by matriarch 1277 during June-August.

This mother-daughter pair remained associated with each other for a minimum of 3-1/2 years after the daughter's birth. Once they regrouped after the fawn rearing period each year, they were in the same group a total of 37 (90%) of 41 times.

(3) We radio-collared the newborn fawns of neckbanded female 2378 in 2 successive years. Female 2378 was an estimated 5 years old when newborn 3079 was captured. After 2378 isolated herself to give birth to 2180, her previous daughter 3079 was not observed with them until 2 September. From that date through April, however, all 3 deer were in the same group during 15 of 16 observations.

Daughter 3079 left the matrilineal group by 4 May at 23 months of age, while 2378 and her 11 month old daughter 2180 remained together until 3 June. On 5 June, the yearling was alone, but was with her 2-year-old sister on 10, 12, and 24 June. From that time, until 2180 lost her collar on 15 August, none of the 3 females were observed together. The radio collar on 3079 also ceased to function about that time.

Female 2378 was next observed on 21 September 1981, with 2 other females and 2 fawns. One of the adult females was wearing a fawn-type radio-collar and was presumed to be 3079. These 2 deer were observed together all 5 times that 2378 was reobserved during the rest of that biological year. On 30 December 1982, the same 2 deer were observed together and the adult with the fawn-type radio-collar was recaptured, verified as 3079, and marked with an individually recognizable neckband. Reobservations were few from that time through spring 1987, but 2378 and 3079 were in the same group during 16 of 17 times they were seen from autumn through spring. They were not together during any of 3 summer reobservations, but were observed together by September in both 1983 and 1984. This mother-daughter combination continued to associate with each other through 8 years of age for the daughter.

(4) Data on associations of female 2479 and her daughter 3679 were collected through 5 years of age for 3679. Mother and yearling daughter were no longer together by 8 June. The mother was always observed alone through 18 June and was not observed with new fawns. On 25 June and 3 July she was observed with a yearling male, indicating that she probably did not have fawns. Mother and daughter were first reobserved together on 8 August, but occurred in the same group during only 6 (30%) of 20 observations through the remainder of that biological year.

Both mother and daughter reared fawns during the following year, however reobservations were few because neither retained a functioning radio-collar. They were first reobserved together, with their fawns, on 28 August and were

together during 6 of 9 observations through the rest of that biological year. They were observed together only 1 of 6 times during autumn through spring over the next 2 biological years.

This mother-daughter combination, although continuing to use the same general home range area (Fig. 7.13), had the least degree of association of all marked mother-daughter pairs. They were in the same group during only 13 (37%) of 35 observations during autumn through spring periods for the daughter's ages of 1-4 years.

(5) Female 6581 was marked with a neckband only, but her daughter 6381 wore a radio-collar. The daughter was first observed apart from her mother at 11 months of age on 13 May 1982. They remained separated through 24 June, after which radio contact with 6381 was lost. Because attempts to relocate 6381 were unsuccessful through July and August, she apparently had dispersed off the study area during that time. She may have returned to the area anytime after August, but was not re-observed until 26 December 1982. She was first seen with her mother on 2 February 1983. Thereafter, mother and daughter were together during all of 7 observations until 8 June when they again separated. They were next observed together on 4 August 1983 and each had a single fawn. From that time, until 23 February 1984, mother and daughter were together 15 of 19 times they were observed. The mother was never reobserved after 23 February 1984.

(6) Female siblings 1582 and 1682 were the daughters of female 1681. From family breakup on 18 May 1983 through 22 August 1983, when they were first reobserved with their mother, the sisters were together only 4 of 11 times either was observed. Once reunited with their mother, they were together in 15 of 19 observations through 19 March 1984 when 1582 was killed by a coyote. During that period, 1582 was with her mother on 13 of 19 observations and 1682 was with her mother on 14 of 19 observations. When not with their mother, these siblings were together 3 times, alone once each, and with female 1481 (of unknown relationship, but usually with matriarch 1681) the remainder of the time. From the time 1582 was killed through 28 May 1984, 1682 was with her mother 4 of the 5 times she was observed. Female 1681 and her daughter 1682 were next observed together on 20 October 1984. They were in the same group during 3 of 4 subsequent reobservations.

Association of Sisters

Three cases involving the association of sisters were described with mother-daughter relationships. An additional 3 sets of twin females were broken up when one of the sisters

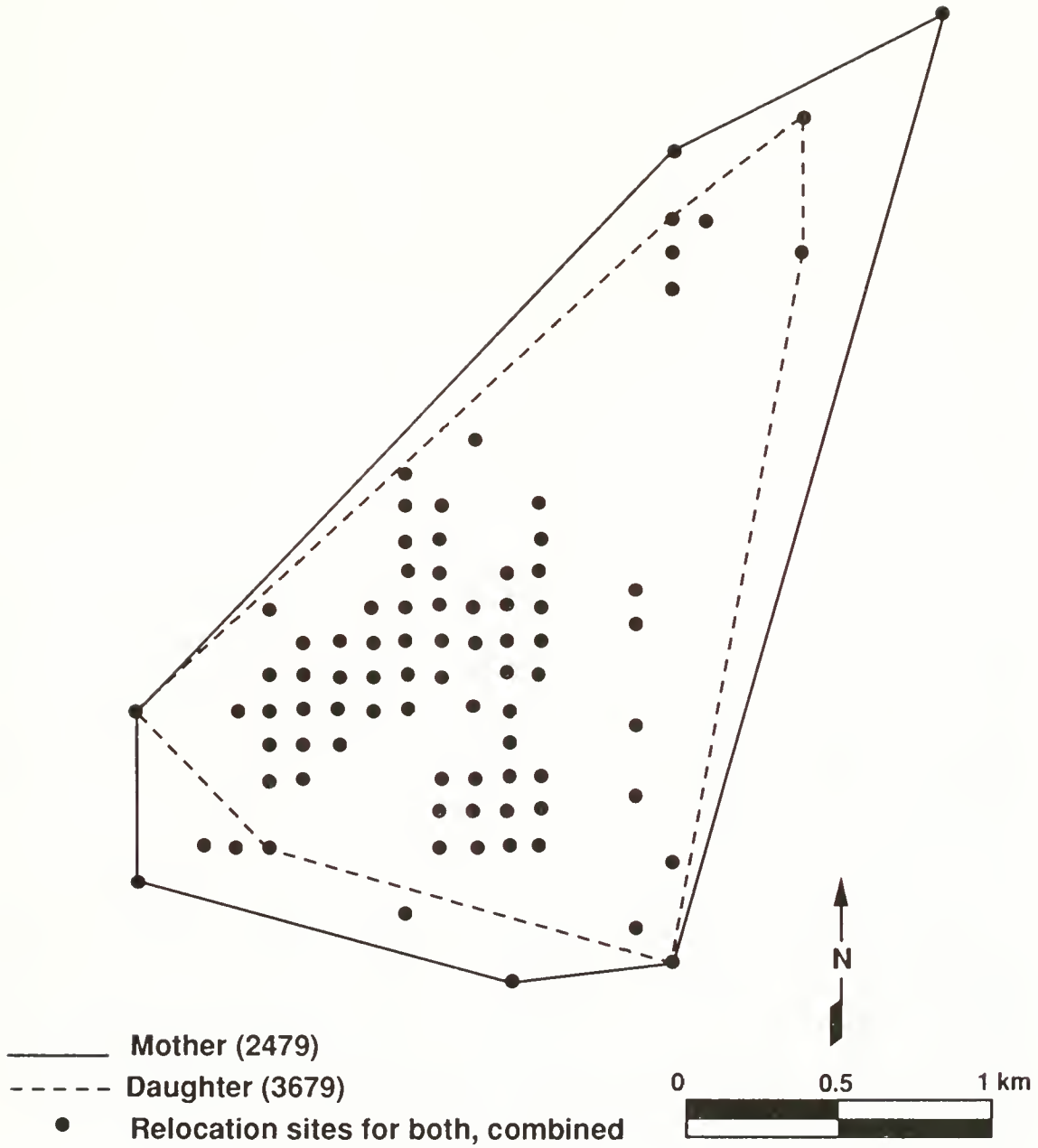


Figure 7.13. Home range boundaries and relocation sites for female 2479 and her daughter 3679.

dispersed from the study area while the other did not. One case of marked sisters also occurred as part of a set of triplets.

The relationship of triplet male 3680 with his sisters, 3480 and 3580 was discussed previously. The sisters were most often apart during the first month following family breakup but thereafter were usually in the same group through their second year. Family breakup occurred on about 23 May 1981. On that date, female 3580 and male 3680 were together, but female 3480 was separate from her siblings. All were separated on 29 May, but on 3 June female 3580 and male 3680 were back together. All 3 were separated on 5, 8, 12, and 18 June, but the sisters were together on 10 June. Thus, during the period 23 May to 18 June, the sisters were together only 1 of 8 times that they were observed. From 24 June 1981 until 1 May 1982, near the start of their first fawning season, they were together 13 of 17 times that they were observed.

During their third year (1 June 1982 through 31 May 1983), the sisters both had their first fawns; in each case, a singleton that appeared to survive through 1 year. They were observed 13 times that year, but never in the same group, although on 29 July 1982 they were observed about 100 m apart, each with her young fawn.

During their fourth year (starting at 3 years of age) the sisters were observed 3 times during June and July but were never together. From 4 August through 14 December 1983, they were together 5 of 11 times they were observed. Both either had not had or, more likely, had lost their fawns by 4 August 1983. Female 3480 was collected on 14 December 1983, ending further possibilities of association. Female 3580 has remained on or near her natal area through 1987.

Associations of Marked Deer of Unknown Family Relationship

Two mature males, observed from January 1979 through October 1980, were closely associated with each other except during the rut. During January-October, the two were in the same group during 24 (59%) of 41 observations over the 2 years. The association was strongest during late February through May, when they were together 14 of 16 times either was observed. Although these 2 mature males were frequent associates, based on the dispersal rates of yearling males, it is unlikely that they were maternally related.

There were several instances of marked females associating frequently with each other when the family relationship of the individuals was unknown. In the previously described relationship involving female 1277 and her daughters 1077 and 1177, another marked adult female

(1377) of unknown family background, was frequently in the same group. The 4 were captured as a group during February 1977. Female 1377 rejoined the group in mid-December 1977 and 1978, after 1277 and her daughters had regrouped. From spring 1977 through spring 1979, after the 2 older females had joined the group, they were together during 31 (84%) of 37 observations. On the occasions when the daughters of 1277 were not with her, they were often with 1377. Although the relationship of the 2 older females was unknown, based on their ages it is likely that 1377 was a younger sister or previous daughter of 1277.

A similar situation existed in the previously described relationship of female 1681 and her daughters 1582 and 1682. Another marked mature female (1481) was often associated with this marked mother-daughter combination. From the time the 2 mature females reassociated with each other by early winter each year until the next parturition period, they were together during 38 (75%) of 51 observations. Again, when the twin yearling daughters were not with their mother, they were often with 1481. Based on the age of 1481 at capture, she could have been a previous daughter of 1681 (older sister of 1582 and 1682).

In 1980, twin male fawns (2880 and 2980) of female 1577 were captured and radio-collared. One of a set of twins (female 3080) of an unmarked female was captured and radio collared at the same time, near the same area. During summer and autumn, these 2 sets of twins and their mothers had overlapping home ranges (Riley and Dood 1984), but did not group together. From 13 February 1981 until 29 May 1981, all marked deer, and presumably the mother of 3080, were together 4 of 7 times they were observed. The yearling males both dispersed from the study area at 1 year of age. The yearling female was reobserved with female 1577, her new fawns, and other unmarked deer on 14 October and 3 November 1981, but lost her radio collar within a week of the last relocation. On 29 December 1982, 3080 was recaptured and refitted with a radio collar. For the next 2 winter-spring periods, 1577 and 3080 were together 11 of 17 times they were reobserved. Although 3080 was not the daughter of 1577, it is possible that her unmarked mother was maternally related to 1577.

Summary and Discussion

The spatial distribution deer on the area was clumped or aggregated and not uniform or random. "Core blocks" appeared to support relatively stable numbers of deer, and most fluctuation in deer numbers occurred in areas adjacent to and distant from those "core blocks". It was apparent that not all areas and habitats provided for equal production and survival of deer and that the stable "core blocks" observed

were areas that had been preempted by established matriarchs. Home ranges that included the stable "core blocks" were passed on through the matrilineal family. As long as the matriarch remains alive, however, female fawns must establish their own "parturition territory" (Ozoga et al. 1984) in areas adjacent to that of their mother. Thus, "core blocks" become larger "core areas" and include the "parturition territories" of several generations. The pattern of dispersion for the population indicated that in rapidly increasing populations, marginal habitat is filled as female fawns recruited in "core areas" must establish their own "parturition territories" at some distance away from that of the original matriarchs. All of this leads to a density distribution (Fig. 7.1) that appears as aggregated areas of high use surrounded by roughly concentric areas of lower, declining use. Mature males and yearlings of both sexes were relegated to areas not preempted by productive females.

It was apparent that not only did different sex and age classes most often occur in different social groups, but they also tended to occupy different land areas during most of the year. Thus, for many analytical purposes, the different sex and age classes should be viewed as separate populations rather than as a homogeneous "mule deer population". Clutton-Brock et al. (1982) also indicated that male and female red deer, at least, should be viewed as separate populations. For some analyses, it may be valid to treat mature females and their fawns, non-productive females, yearling males, and mature males as 4 separate populations.

Collectively, the information from marked deer indicated that matrilineal groups are the predominant social group for mule deer in the Missouri River Breaks. The predominance of matrilineal social groups and their structure was very similar to that reported for white-tailed deer by Hawkins and Klimstra (1970) and Ozoga et al. (1982a). The association of mother and daughter was known to last a minimum of 8 years. The relatively low level of dispersal by yearling females contributed to the formation of matrilineal groups. The degree of association between mother and daughter generally declined with age, but that was probably primarily related to the increasing likelihood that the daughter had her own fawns and became more likely to form her own matrilineal group. When both mother and daughter recruited fawns, reassociation often did not occur until mid-to-late-winter. Data on group characteristics from the entire population also indicated that females were less likely to group with other females when fawn survival was high. However, a 12-year-old female and her 7-year-old daughter were known to reassociate by early autumn when neither had living fawns. Matrilineal groups were known to contain a minimum of 3 generations; a matriarch, her daughter(s), and fawns of both the matriarch and her previous

daughters. We strongly suspected that some groups contained at least 4 generations; including at least 3 adult generations and the fawns of females 2-years or older.

Sisters, both twins and sisters of different ages, were closely associated, often occurring in the same matrilineal group, especially if at least one did not have fawns. We were not able to determine the associations of sisters in cases where the matriarch was dead, but combined information from marked deer indicated that sisters were somewhat less closely associated than mother-daughter combinations.

The only other social group we observed with a potential for relatively long-term stability occurred among mature males. Our data on these groups were limited, but males were commonly observed in groups from late January through early October, and some individuals were relatively closely associated with each other during that period. Agonistic behavior of mature males toward each other during the breeding season disrupted these groups, but they re-formed by late January or early February. High hunting mortality limited the opportunity for long-term association of individual males, thus lessening the likelihood of long-term stability.

There was a tendency, at least during summer and autumn, for females with fawns and mature males to be socially and spatially separated. That indicated social and physiological requirements may differ between sexes (Verme 1988) and that competition for forage and cover between males and their offspring probably was reduced.

Because 70% of yearling males emigrated from their natal home ranges, the opportunity for inbreeding was reduced considerably. Additionally, as a result of several causes, primarily pre-rut hunting mortality, a minimum of 4 of 17 non-dispersing males were known not to have bred with their mothers or sisters. Based on suspected additional hunting loss, that number probably was higher. Including the dispersing males, a maximum of 23% of yearling males could have possibly bred with their mothers or sisters. Although a small percentage of yearling males remained on or near their natal range, matrilineal groups did not contain males. In one case, a yearling male was in the same group as his mother in autumn prior to the rut, but no males were ever observed with their mother during or following their first rutting season.

The low rate of dispersal by yearling females made father-daughter incest theoretically more likely than son-mother or brother-sister incest. The high rate of hunting mortality for mature males reduced that theoretical probability considerably, however. The father faces the last part of a hunting season after the daughter is conceived and

then 2 winters and a full and partial hunting season before she reaches breeding age. The statistical probability of the father living to the first breeding season for the daughter is 28%, based on average mortality rates observed during this study. Survival probabilities for the father decline considerably from that for subsequent breeding seasons. Probability of inbreeding is relatively small for this population, but the fact that at least some potential for inbreeding remains may be beneficial (Shields 1983).

The occurrence of matrilineal groups probably had several survival advantages that outweighed the disadvantage of increased resource competition within an area. As population numbers increase, additional deer put increasing pressure on the resources of an area. When mature females allow their female offspring to rejoin them after early fawn-rearing, thereby forming matrilineal groups, they ensure that the resources within their home range, although somewhat diminished for them, are beneficial to and passed on to their genetic heirs rather than to unrelated deer. Kin-selection principles (Maynard-Smith 1964 and Hamilton 1964) can explain much of the rationale for the formation of matrilineal groups.

Matrilineal groups are also especially beneficial to the offspring of deer that only move to "winter range" during the most severe winters. Continued association with the matriarch ensures that they will eventually learn the location of "winter ranges". The fact that yearling males are primarily associated with female groups also increases the chances that they will learn the locations of "wintering areas" even though they are usually genetically unrelated to the female groups. This may also be beneficial to the females because they are increasing the survival odds of a potential mate of new genetic stock.

Our data enabled us to address the issue of factors determining group size as discussed for white-tailed deer by Hirth (1977). The general consensus has been that group size varies with habitat type and that relationship evolved as a means of minimizing losses to predation and possibly optimizing feeding efficiency. Our data indicated that other factors also are involved. Further, the general perception that mule deer are more gregarious than white-tailed deer (DeVos et al. 1967) may not result from inherent social differences, but rather is related to differences in habitat use and fawn survival.

The habitat on our study area was a mixture of moderately dense cover interspersed with relatively open forest cover and very open shrub-grasslands. Deer had a variety of cover options, but dense cover was limited. Our data indicated that group size for adults was dependent on fawn survival. Females

tended to remain solitary as long as their fawns survived, although regrouping with yearling daughters was common after the fawn-rearing period. When both the matriarch and her daughters of fawn-bearing age recruited fawns, they often remained apart; if they regrouped, it was usually during late winter or spring. Fawns, the deer most vulnerable to predation, occurred in the smallest social groups; larger groups contained mostly adult deer. Because solitary females and their fawn(s) primarily used relatively denser cover (Riley and Dood 1984), the predator avoidance hypothesis that large ungulates are most likely to avoid detection by predators in dense cover when alone or in small groups seemed to hold. During the first 45 days of life, however, females and fawns made considerable use of open habitat (Riley and Dood 1984) and did not group with other deer.

The only time that deer made extensive use of open habitats was during spring when feeding on ubiquitous new growth that appeared first in open habitats. For the limited time period that larger groups fed together on open areas, forage competition was not a problem. The most efficient way to use the high density of available food and detect predators was probably to feed in large groups. These groups were only temporary feeding aggregations and after feeding, the deer separated into smaller family groups when they moved back to denser cover to bed.

We concur with Hirth (1977) that both predator avoidance and optimum feeding efficiency considerations may interact with habitat type to help determine group size. However, our data indicate that, in areas where a choice of habitat type is available, females with fawns prefer solitude and may preempt denser cover. The most observable groups are the larger groups that often use more open habitat, however, these larger groups did not necessarily prefer or always use open habitat. On our area, larger group size was more related to poor fawn survival than to the type of habitat the deer were using. Thus, in late summer and early autumn 1985, deer were in larger groups than usual even though they were not using more open habitat than normal. It is possible that the larger group sizes Hirth (1977) observed on the Welder Refuge as compared to the George Reserve were at least partially related to the poorer fawn survival on the Welder Refuge as compared to the George Reserve.

We agree with Hirth (1977) that density of deer did not affect group size. On our area, the largest groups were observed during years of poor fawn survival that included years of both high and low deer density. However, we do not agree that mule deer are inherently more gregarious than white-tailed deer (DeVos et al. 1967). Very small family groups appeared to be the preferred social group, especially

as long as fawns survived. Both Wood (1987) and Hirth (1977) reported larger average and maximum group sizes for white-tailed deer in prairie habitat and open river bottom habitat, respectively, than we observed for mule deer. The perception that mule deer are more gregarious than white-tailed deer may reflect the fact that many reported studies of mule deer were in relatively open habitat and/or were conducted during periods of poor fawn survival.

CHAPTER 8

HOME RANGE AND MOVEMENTS

Home range characteristics were determined from 6395 relocations of 135 radio-collared deer monitored during 1976-1984. Eighty-three of those deer were first radio-collared as newborn fawns; 30 of those also contributed home range information as adult deer. The remaining 52 radio-collared deer provided data on home range characteristics of adults. A total of 76 individual adult females and 6 adult males provided data for calculation of adult home ranges.

Home range size and deer mobility were determined by 2 methods, the polygon home range (Mohr 1947) and average activity radius (Robinette 1966). The polygon home range (PHR) usually overstated home range size by including non-habitat within home range boundaries, but had the advantage of being a commonly used technique which facilitates comparisons. We used PHR to estimate home range size rather than various statistical methods because deer on this area did not use the environment in a bivariately normal manner and because statistical methods often "provide estimates that distort and obscure real biological phenomena" (Smith 1983). The average activity radius (AAR) was not a good measure of home range size or shape (Jennrich and Turner 1969) but gave a general measure of mobility by computing average distance of relocations from a geographic activity center.

Home range size was calculated for 5 time periods. Life home range was calculated for 41 adult females and included only those deer monitored for 24 months or more. Mean number of relocations was 84.2 (range, 29-192) and mean number of months of continuous data was 46 (range, 24-85). Correlation analysis and plotted data indicated that once at least 29 relocations were made over a 24 month period, neither PHR nor AAR significantly increased ($P>0.05$) as number of relocations or number of months of observation increased. Once 24 months of radio-relocations were obtained, all observations of those deer were included in calculations of life home ranges, including those made after the radio-transmitter ceased functioning.

Annual home ranges included relocations between 1 June and 31 May (biological year). Sixty-seven annual home ranges were calculated for 36 females, and 6 were calculated for 5 adult males. Mean numbers of relocations for annual home ranges were 28.7 (range, 19-50) and 25.0 (range, 16-32) for adult females and adult males, respectively. Summer home ranges for adult deer included observations from 1 May through 30 November. Ninety-nine summer home ranges were calculated for 48 females and 7 for 5 adult males. The mean numbers of

relocations were 17.5 (range, 10-38) for adult females and 13.7 (range, 11-19) for adult males. Winter home ranges included relocations from 1 December through 30 April. One hundred-eleven winter home ranges were calculated for 70 females and 4 for 3 adult males. Mean number of relocations during winter was 10.6 (range, 8-20) for adult females and 10.5 (range, 8-13) for adult males. Summer home ranges for fawns included all relocations from 13 June through 22 September. Only those fawns that survived through at least late August were included in home range analysis. Mean number of relocations for 83 fawns was 18.9 (range, 8-31).

Two types of movement patterns were determined for adult females. Yearlong residents could be found in any portion of their home range at any time of the year, though certain portions received more use during some seasons than others. Deer having distinct seasonal ranges that fit Baker's (1978) characterization of migratory movements moved regularly on a seasonal basis between areas separated by a minimum of 3 km. Migratory deer moved a maximum of 8.8 km between seasonal ranges. They were almost always deer that used the southern edge of the study area (near the prairie) during summer and moved during autumn and winter to areas near the river with much steeper topography and with both north- and south-facing slopes. Migratory adult females had significantly larger PHR and AAR (Mann-Whitney tests, all $P<0.01$) than yearlong resident adult females for life, annual, summer and winter periods (Table 8.1).

A striking characteristic of home range measurements for all classes of deer and all periods, was the extreme individual variability in home range size and movements. The range of values in Table 8.1 indicated that not only do values overlap considerably between categories and seasons, but a wide range of values existed within each category in each season. Wide seasonal and annual variation of home range size was true even for individuals. Because of this extreme variation, only large differences in values were statistically significant. The annual PHR for migratory female 1577 varied from 4.55 to 16.64 km^2 over a 5 year period, and the annual PHR for resident female 1480 ranged from 2.14 to 5.17 km^2 over a 3 year period. The summer PHR of migratory female 1577 ranged from 3.69 to 9.77 km^2 over 5 years, and the summer PHR of resident female 1580 varied from 1.68 to 4.48 km^2 over a 3 year period. The variation in annual and seasonal home range size for individuals was not the result of differences in the number of relocations during the period. Similar numbers of relocations were made annually for most deer and PHR size did not increase with increased number of relocations for those deer at the extremes. For example, the smallest annual PHR for female 1577 (4.55 km^2) was during the year we made the most relocations (50) of her. During the year we made the

fewest relocations (22), her PHR was twice as large (9.35 km^2).

Factors Affecting Home Range Size and Use

Migratory deer had larger home ranges than resident deer, but we also examined the influence of deer density, sex and age of deer, fawning status of females, forage production, and habitat on home range size. Additionally, non-quantifiable influences such as tradition and chance were considered.

Both PHR and AAR were significantly larger (Mann-Whitney tests, all P's <0.01) for adult males than for all adult females, annually and seasonally (Table 8.1). The home range size for a stag (castrated or non-descended testicles) was intermediate to those of adult females and adult males, but closer in size to those of adult males (Table 8.1).

To reduce variability, we used only yearlong resident females to test the effect of reproductive status on home range and movements. Females with fawns were not as mobile as those without fawns (Table 8.2). Females with fawns that survived throughout summer had a significantly smaller mean PHR (2.34 km^2, n=23) than those without fawns (4.50 km^2, n=27; M-W Rank Sum = 369.0, P<0.01). Mean AAR also was significantly smaller (M-W Rank Sum = 418.5, P<0.01) for females with fawns (0.72 km) than for females without fawns (0.92 km). Because this relationship occurred across all years, densities, forage conditions, habitats, and age classes, the presence of fawns-at-side overrode all other factors in determining the home range size of adult females.

Our data did not support the assumption that females would have smaller home ranges as density increased (Table 8.2). Four density classes were chosen; 1976-78 ($\bar{X}$ = 310 adult females, range 290-335), 1979-80 ($\bar{X}$ = 488 adult females, range 425-550), 1981-82 ($\bar{X}$ = 690 adult females, range 680-700), and 1983-84 ($\bar{X}$ = 775 adult females, range 760-790). Summer home range size of resident adult females was not significantly different among density classes (Kruskal-Wallis; PHR (X^2=3.43, P=0.33, df=3) and AAR (X^2=0.08, P=0.99, df=3)].

For most categories, sample size was too small to partition the effect of reproductive status and density. A sufficient sample was available to compare only resident females that did not have fawns in 1979-80 (Table 8.2, n=7, mean density = 488 females) to those that did not have fawns in 1983-84 (n=10, mean density = 775 females). Neither PHR ($\bar{X}$ = 4.32 km^2 and 4.29 km^2) nor AAR ($\bar{X}$ = 0.94 km and 0.89 km) were significantly different for 1979-80 and 1983-84, respectively (Mann-Whitney, Rank Sum =72.0 P=0.41; Rank Sum=64.0, P=0.96).

Table 8.1. Home range size and mobility of adult mule deer on the Missouri River Breaks study area, Montana.

	Life Home Range			Annual Home Range			Summer Home Range			Winter Home Range		
	N[a]	PHR[b]	AAR[c]	N	PHR	AAR	N	PHR	AAR	N	PHR	AAR
Adult Females												
Non-migratory	25	8.3±1.41[d] (4.3-17.8)[e]	0.89±0.07 (0.66-1.32)	41	5.2±1.0 (1.5-17.3)	0.90±0.07 (0.54-1.63)	58	3.4±0.5 (1.0-11.8)	0.83±0.06 (0.46-1.35)	73	2.2±0.2 (0.6-5.8)	0.83±0.07 (0.38-2.64)
Migratory	16	18.4±3.1 (10.8-34.7)	1.5±0.23 (0.94-2.91)	26	8.7±2.2 (1.7-30.2)	1.42±0.23 (0.46-2.79)	41	5.9±1.3 (0.6-16.2)	1.31±0.21 (0.38-3.10)	38	5.2±1.2 (0.8-14.1)	1.51±0.22 (0.47-3.43)
All Females	41	12.3±2.1 (4.3-34.7)	1.15±0.14 (0.66-2.91)	67	6.6±1.1 (1.5-30.2)	1.10±0.12 (0.46-2.79)	99	4.4±0.7 (0.6-16.2)	1.03±0.10 (0.38-3.10)	111	3.2±0.5 (0.6-14.1)	1.06±0.11 (0.38-3.43)
Adult Males				6	27.1±5.2 (16.6-33.4)	2.31±0.39 (1.89-3.17)	7	17.1±5.8 (5.4-29.2)	1.99±0.34 (1.21-2.70)	4	12.1±8.6 (5.0-24.2)	1.88±0.56 (1.24-2.56)
Stag				2	15.6	1.95	2	8.0	1.64	2	12.1	2.1

[a] N = number of calculated home ranges

[b] PHR = Polygon Home Range in km^2

[c] AAR = Average Activity Radius in km

[d] $\bar{x}$±95% CI

[e] Range

Table 8.2. Relationships of summer home range size and mobility of non-migratory adult females to various potentially influencing factors.

	N[a]	PHR[b]	AAR[c]
With fawns	23	2.34	0.72
Without fawns	27	4.50	0.92
1976-78 (ave. density 1.1/km^2)	6	3.20	0.81
1979-80 (ave. density 1.7/km^2)	20	3.41	0.84
1981-82 (ave. density 2.5/km^2)	18	3.06	0.83
1983-84 (ave. density 2.9/km^2)	15	3.91	0.84
Without fawns 1979-80, 1.7/km^2	7	4.32	0.94
Without fawns 1983-84, 2.9/km^2	10	4.29	0.89
Poor forage prod. (1977,80,84)	23	3.48	0.86
Med. forage prod. (1976,81,83)	24	3.72	0.83
Good forage prod. (1978,79,82)	12	2.59	0.77
With fawns-poor forage prod.	8	2.30	0.71
With fawns-good forage prod.	8	2.46	0.78
1-year-old females	20	4.77	0.93
2-year-old females	10	4.56	1.00
3-year-old females	8	3.28	1.08
4+year-old females	40	3.04	0.90

[a] number of adult females
[b] km^2
[c] km

We tested the assumption that home range size and average movements should decrease as forage became more abundant (Table 8.2). Forage production as measured by clipped plots fell into 3 general levels; poor (1977, 1980, and 1984), medium (1976, 1981, and 1983), and good (1978, 1979, and 1982). Although home ranges generally were smaller during good forage years than during poor forage years, the difference was not statistically significant for PHR (K-W, X^2=2.94, P=0.23, df=2) or AAR (K-W, X^2=0.97, P=0.62, df=2).

Females that had fawns during years of good forage production did not have smaller home ranges than those that had fawns during a poor forage production year (Table 8.2; PHR, Rank Sum=67.0, P=0.96; AAR, Rank Sum=76.5, P=0.40).

Data in Table 8.2 indicated decreasing PHR size with increasing age, but no consistent relationship between AAR and

age. We believe that age and reproductive status were too autocorrelated (the chance that a female will have a fawn increases from age 1 to 5, see Chapter 5) to enable us to determine any effects due entirely to age.

Factors Affecting Summer Home Range Size of Fawns

Home range size of fawns on this area from 1976-1980, as determined by the modified minimum area method (Harvey and Barbour 1965), was reported by Riley and Dood (1984). They found that fawn summer home range size decreased with increased population size during 1976-1980.

We found that mean home range size for fawns increased in ascending order as follows: single females, twin females, single males, mixed sex twins, twin males (Table 8.3). Those differences were not statistically significant, however (Kruskal-Wallis; PHR, X^2=1.39, P=0.85, df=4; AAR, X^2=1.43, P=0.84, df=4). Combined, twins had larger home ranges than singles, but the significance level was marginal (Mann-Whitney; PHR, Rank Sum=1361.0, P=0.06; AAR, Rank Sum=1352.0, P=0.08). Mean home range size was larger for all males than for all females, but the difference was not statistically significant (Mann-Whitney; PHR, Rank Sum=874.5, P=0.43; AAR, Rank Sum=875.0, P=0.43). Although the general tendency for differences in movements by sex and litter size appeared to be as expected, the extreme variation in values (Table 8.3) precluded statistical significance.

Home range size of fawns was compared among the same 4 density classes delineated for adult females, and a significant difference in home range size among density classes was observed (Kruskal-Wallis; PHR, X^2=13.77, P<0.01; AAR, X^2=9.27, P=0.03). Summer home range size generally declined as deer density increased. There may have been effects related to variation in sex and litter size among years, but sample sizes were too small to conduct tests which would eliminate those effects.

The comparison of summer home range size for fawns eliminated the effect of reproductive status on home range size that we observed for adult females. Although total summer home range size of adult females did not decline with increasing density, it appeared that the size of the fawn-rearing areas or "parturition territory" did.

There was no evidence that good forage production reduced the movements or summer home range size of fawns. Home range sizes were actually largest during 1978 and 1979 when forage production was best. Sample size was not sufficient to partition the effect of density and forage abundance.

Table 8.3. Summer home range size and mobility of fawns 1976-1984, Missouri River Breaks study area, Montana.

Year	N[a]	Mean + SE PHR[b]	Mean + SE AAR[c]	Range PHR	Range AAR
1976	4	2.3±0.7	0.73±0.07	(0.53-3.76)	(0.58-0.93)
1977	10	2.3±0.4	0.71±0.06	(1.12-5.19)	(0.50-1.10)
1978	9	4.8±0.8	0.85±0.07	(1.03-9.29)	(0.46-1.18)
1979	11	2.5±0.5	0.66±0.05	(0.91-5.95)	(0.43-0.92)
1980	8	1.9±0.3	0.73±0.13	(0.55-3.07)	(0.30-1.10)
1981	14	1.9±0.5	0.61±0.08	(0.24-6.12)	(0.25-1.24)
1982	11	1.3±0.3	0.60±0.08	(0.24-3.41)	(0.22-1.04)
1983	7	1.8±0.3	0.53±0.03	(0.84-2.98)	(0.44-0.63)
1984	9	1.8±0.4	0.77±0.14	(0.44-3.97)	(0.32-1.67)
Total	83	2.3±0.2	0.68±0.03	(0.24-9.29)	(0.22-1.67)

	Mean N	Mean PHR	Mean AAR	Range PHR	Range AAR
Single female	24	1.88	0.61	(0.24-6.12)	(0.22-1.07)
Twin females	6	1.90	0.64	(0.74-3.16)	(0.41-0.82)
Single male	22	2.06	0.68	(0.24-4.33)	(0.25-1.67)
Mixed sex Twins	8	2.23	0.69	(0.44-5.94)	(0.32-1.24)
Twin males	9	2.61	0.73	(0.42-9.29)	(0.35-1.44)
All females	30	1.88	0.62	(0.24-6.12)	(0.22-1.07)
All males	31	2.22	0.69	(0.24-9.29)	(0.25-1.67)
All singles	46	1.97	0.64	(0.24-6.12)	(0.22-1.67)
All twins[d]	36	2.66	0.74	(0.42-9.29)	(0.32-1.44)

[a] number of fawns
[b] km^2
[c] km
[d] Includes 13 sets of twins for which only 1 member was captured and sexed.

Monthly Patterns of Movements

Monthly AAR were calculated for all individuals with 2 or more relocations per month (range 2-13). AAR were partitioned by sex and by age in months and then pooled within those categories to form a population mean AAR for that sex and age.

Because of the wide variation in values, monthly AAR of females were statistically different only for the most extreme differences in values (e.g. June at 13 months of age vs. June, July, and August for 24+ month old females). Relatively large AAR were recorded from 12 to 14 months of age (Fig. 8.1), when the strong social bond established between mother and young was broken as she prepared for and gave birth to a new fawn. This period was typified by wandering, and occasionally dispersal, of the yearling female. The smallest monthly AAR for 24+ month-old females coincided with parturition and fawn-rearing during June, July, and August. One other trend observed for established, reproducing females (movements of fawns also show this) was a seasonal peak in AAR during March, coinciding with movement to summer range by migratory deer. Movements to winter range did not appear as a sharp one month peak because they may occur throughout the period September-February and individuals may move between seasonal ranges several times during the period.

The wide variation of individual values resulted in few significant differences between monthly AAR of males, but 2 significant peaks in AAR were apparent. The first occurred during May, June, and July as the male fawns reached 1 year of age (Fig. 8.2). A high proportion of yearling males dispersed from their natal home range at this time, accounting for an even greater degree of mobility of yearling males compared to yearling females. The second peak in movements was during the rut in November when the AAR for males was about 3 times that for females. Average activity radii may be larger for males than females during most months, but sample sizes were too small to verify that.

Emigration

Emigration rates of marked yearling males (Table 7.7) were not related to population density. Total numbers of yearling males in the fall population did not change much from that expected, based on recruitment, despite average emigration of 51% of all yearling males from the study area by 14 months of age. Thus, for yearling males, emigration was apparently balanced by immigration.

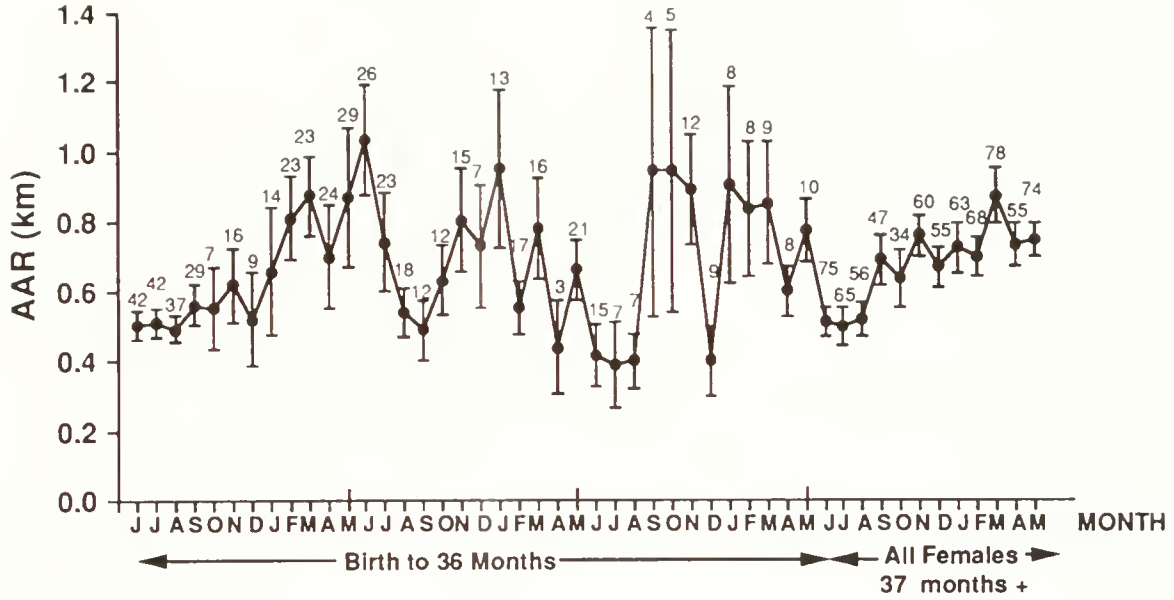

AAR (km)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
MONTH
Birth to 36 Months
All Females
37 months +

Figure 8.1. Monthly average activity radius for females, birth to 36 months, and then by month for all females 37 months and older. Bars represent the standard error of the mean and numbers represent the sample size per month.

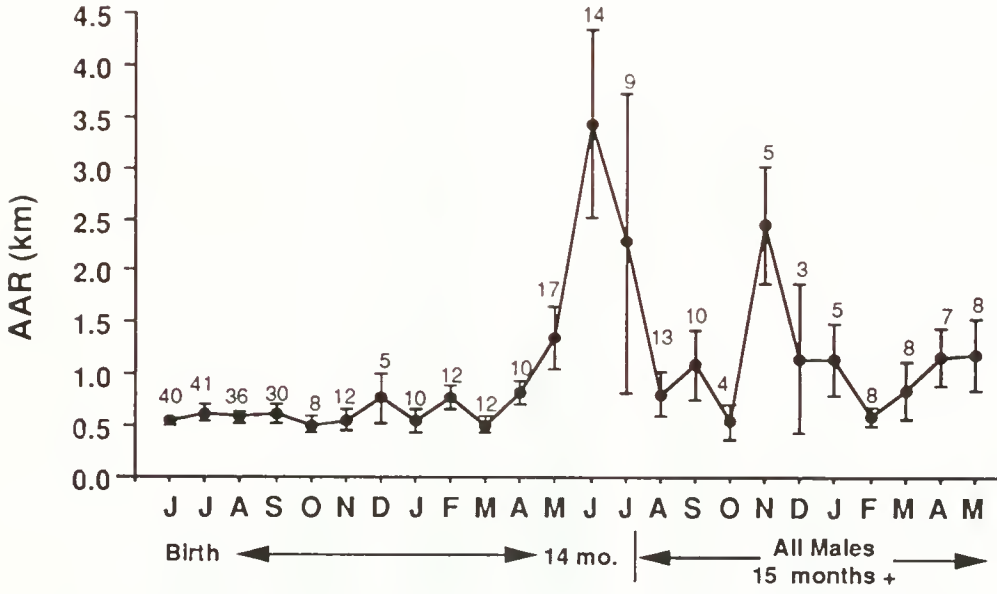


Figure 8.2. Monthly average activity radius for males, birth to 14 months, and then by month for all males 15 months and older. Bars represent the standard error of the mean and numbers represent the sample size per month.

Most dispersal of marked yearling females fit the description of pre-saturation dispersal (Lidicker 1978). Seven of 9 dispersals by marked yearling females occurred during the first 2 years of population increase. Only 2 radio-collared yearling females occurred among the 1986 cohort; both emigrated from the study area. Population estimates indicated that up to 49% of the 1986 female cohort emigrated during summer 1987 without an offsetting immigration. Dispersal during other years was low or non-existent. Contrary to what was observed for yearling males, emigration of yearling females did not appear to be balanced by immigration during any year, although some immigration may have occurred during autumn 1983.

The average date of dispersal was earlier for yearling males than for yearling females (Fig. 8.3). Some yearling males dispersed before their mother was actively aggressive towards them, while few yearling females dispersed until their mothers aggressively chased them. Yearling females stayed in the same area as their mothers for some time, and active aggression on the part of the mother was necessary to break the close social bond that characterized doe-fawn relationships during the first year. Yearling males appeared to be inherently inclined toward dispersal but yearling females did not.

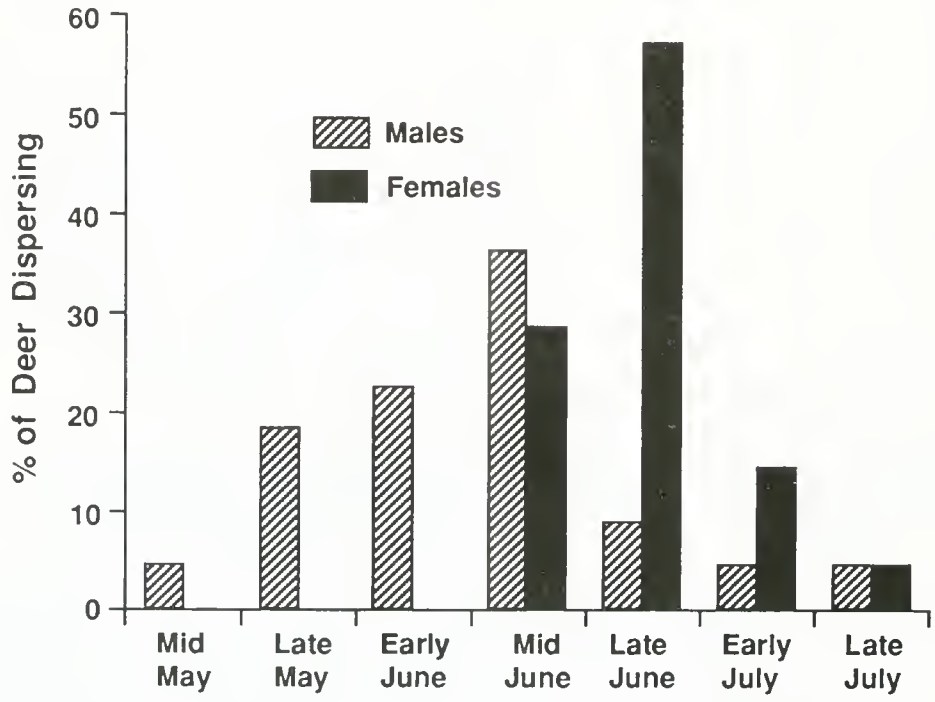


Figure 8.3. Date of dispersal for yearling mule deer.

Dispersal distance averaged 25.7 km and ranged from 7 to 83 km for 21 yearling males (Fig. 8.4). For 7 yearling females, mean dispersal distance was 36.9 km, and the range was 5 to 69 km (Fig. 8.5). The direction of dispersal for yearling females was random (Rayleigh's $Z=0.29$, $P>0.50$), but that for yearling males was non-random (Rayleigh's $Z=8.48$, $P<0.001$). Dispersal by yearling males was bimodal; most males dispersed in westerly and easterly directions, staying within "river breaks" habitat.

Individual Strategies

To further understand factors affecting movements and home range size and shape, plots of home range size, shape, and intensity of use for individuals were instructive. Closely overlapping home range polygons for 5 consecutive years (age 5-9) of resident female 2679 are displayed in Fig. 8.6A. There was relatively little annual variation in home range size, shape, or pattern of use, but annual PHR size ranged from 2.7-4.8 km^2. Intensity of use of the home range area was not uniform (Fig. 8.6B). A 1.7 km^2 area in the southern portion of the home range (24% of 7.1 km^2 life home range) contained 50.3% of all relocations of this female. The northern portion of her home range contained more steep, south-facing slopes than the southern portion and although the northern area was used yearlong to some extent, it was consistently used only during periods of winter when snow was deep. Statistical methods of home range analysis often reduce or overlook the importance of these less intensively used areas that are vital to the survival of deer. These "auxiliary winter ranges" were usually poor in forage quantity and quality and were less intensively used yearlong, but provided some forage, stable footing, and warm microsites during periods of cold temperature and deep snow.

Life PHR for migratory female 1577 (age 3-4 and 6-10 years) was 19.9 km^2 (Fig. 8.7). Annual PHR varied from 4.6 to 16.6 km^2; the smallest and largest annual PHR occurred during years with the mildest and most severe winters, respectively. Female 1577 (Fig. 8.7) spent most of the spring-summer period in the most southern portion of her home range, but during autumn, a majority of her time was spent in an area about 3 km north of her "summer range". Most winter relocations were in or adjacent to the northern portion of the autumn area of use (Fig. 8.7). During periods of very deep snow, she moved to auxiliary wintering areas of very steep terrain north of her normal winter range.

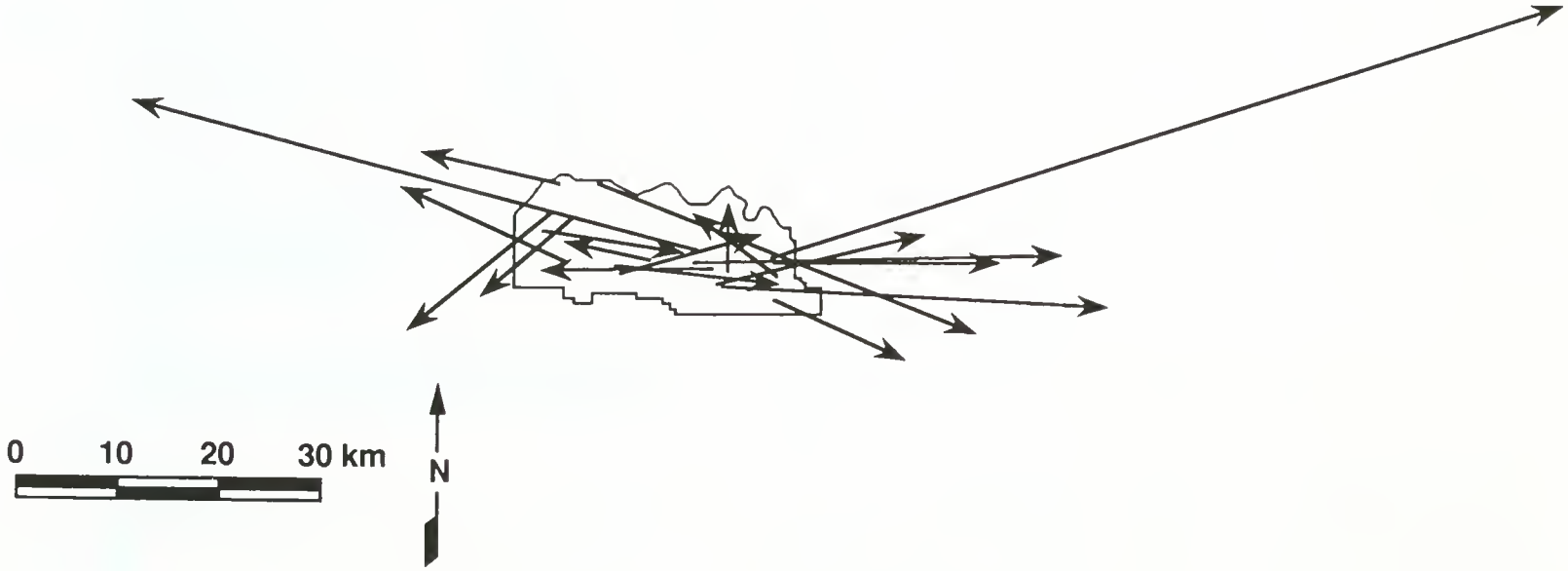


Figure 8.4. Direction and distance of dispersal from the natal area for yearling males with a known end point of dispersal.

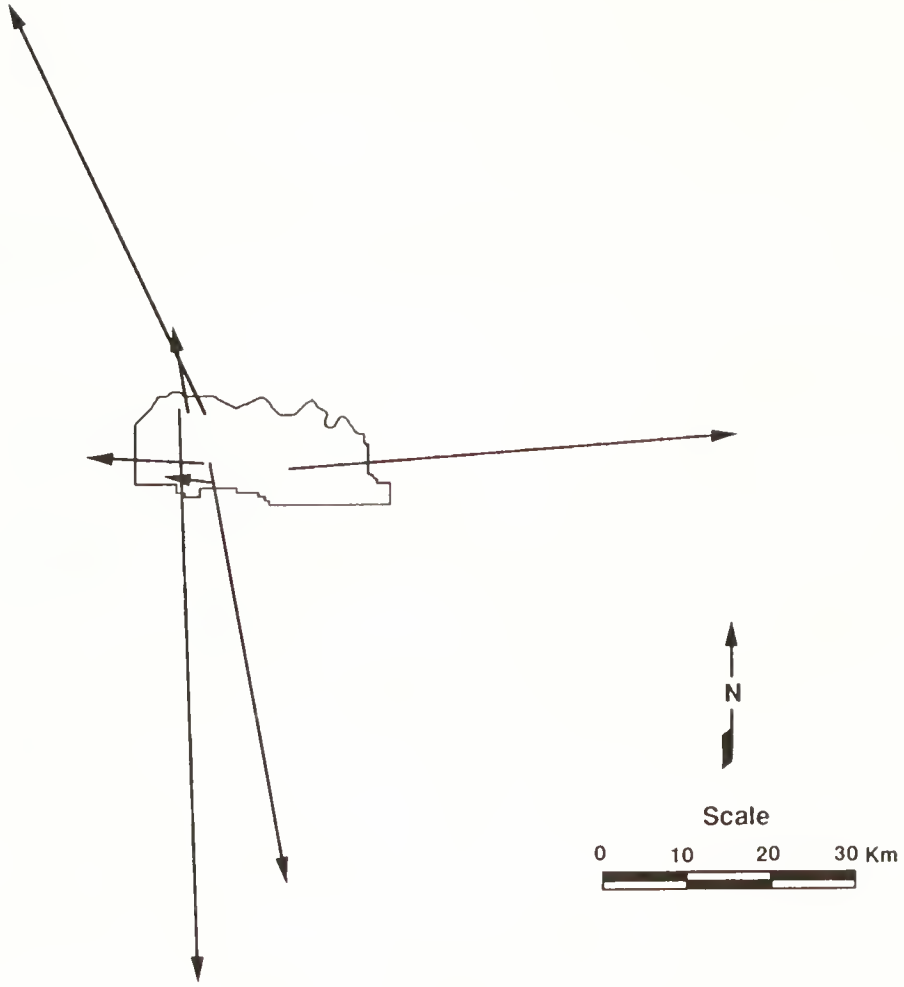


Figure 8.5. Direction and distance of dispersal from the natal area for yearling females with a known end point of dispersal.

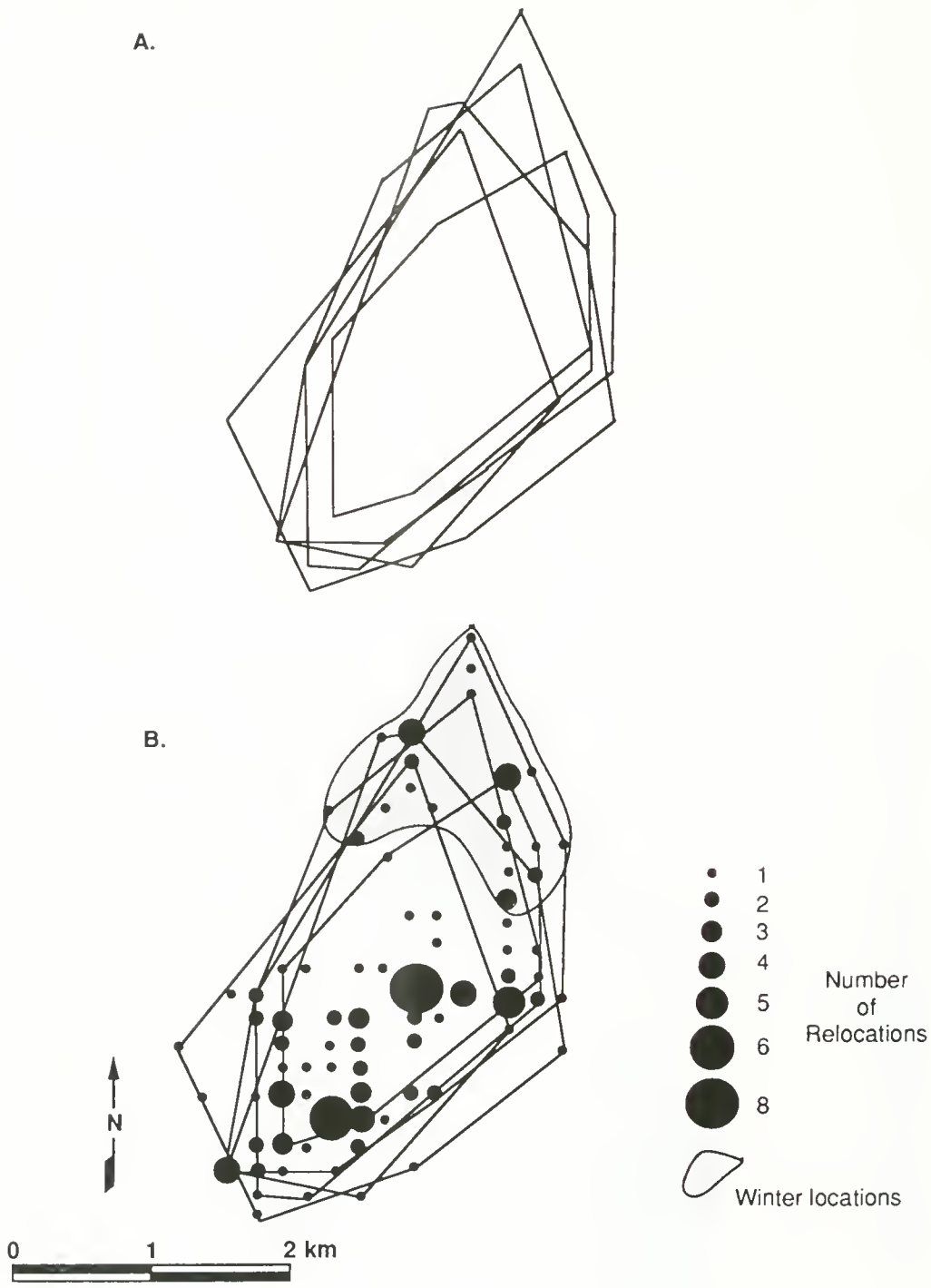


Figure 8.6. A. Annual home range perimeters of resident female 2679 for 5 consecutive years (age 5-9). B. Annual home range perimeters and intensity of use plot for female 2679.

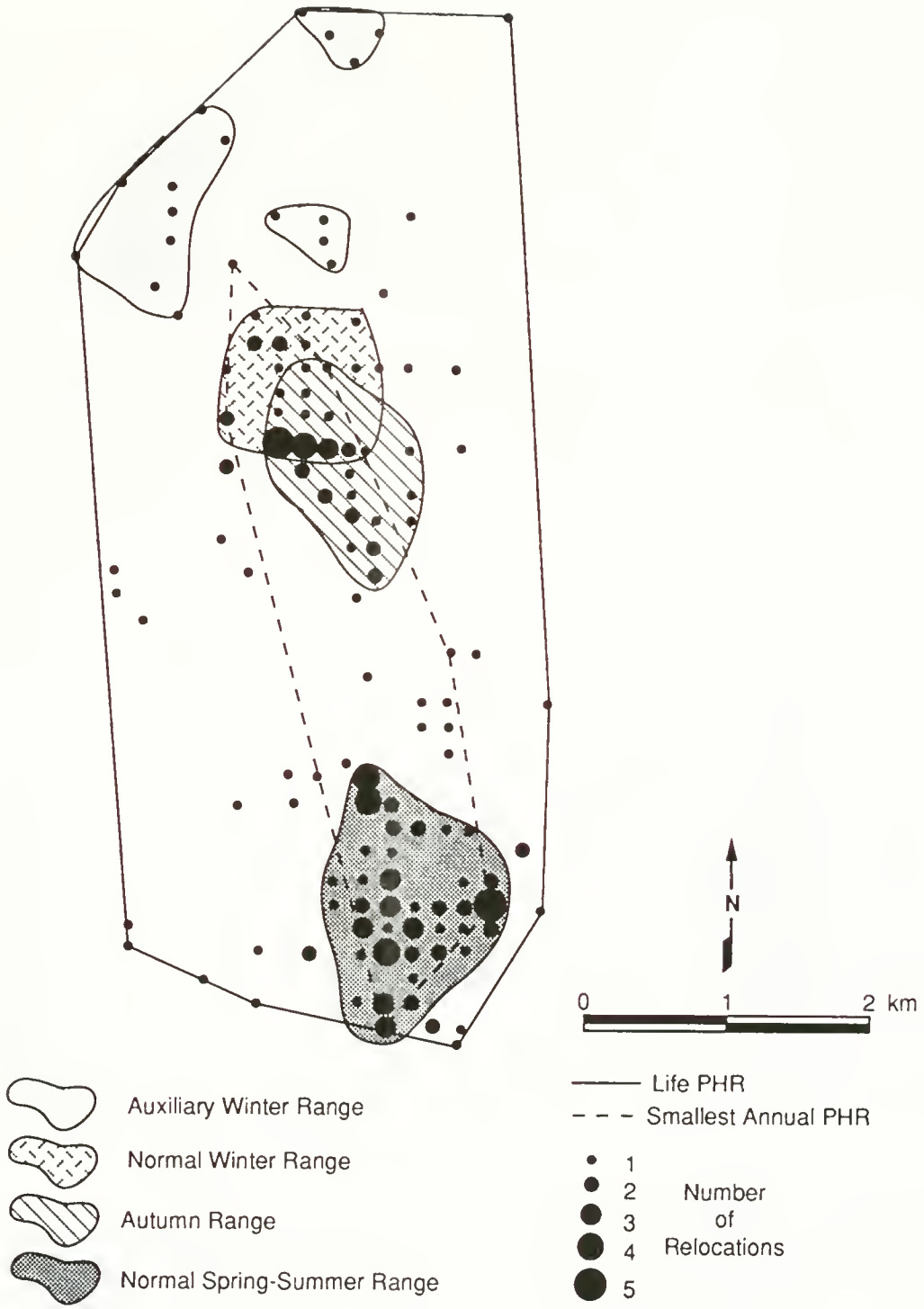


Figure 8.7. Life home range perimeter, intensity of use plot, and seasonal ranges of migratory female 1577.

Seasonal use was not exclusive to an area, even for migratory deer. Rather, a preponderance of seasonal use was within an area. For example, 79% of spring-summer observations of female 1577 were in the southern portion of her home range and 81% of autumn-winter observations were in the northern portion of her home range. Half of the 21% of spring-summer relocations that were on "autumn-winter range" occurred during the dry summer of 1980 when she apparently made use of the more abundant succulent forage still available on steep, north-facing slopes not grazed by cattle on the northern area.

The intensity of use pattern for this migratory deer (Fig. 8.7) was even less uniform than that for a resident deer (Fig. 8.6B). A total of 29.1% of all relocations were within a 1.4 km^2 area of autumn-winter range and 39.6% of all relocations were within a 1.2 km^2 area of spring-summer range. Combined, 68.7% of all relocations of female 1577 during 5 years were within an area that comprised 13.3% (2.6 km^2) of the life PHR. Although not intensively used over the 5 year period, other areas were important to the survival of this deer. Auxiliary winter range areas in the northern portion of her home range were used during periods of deep snow. Those areas included the most northern portion of her PHR, used only during the extremely severe winter of 1977-78.

Areas not intensively used by this deer were probably important in that they represented the process of finding alternate winter areas and areas where forage remained succulent longest. Almost all deer occasionally displayed unusual or unexplainable temporary movements outside of normal home ranges. Some movements may have been related to undocumented disturbances, but also may have been random exploratory movements that resulted in familiarity with alternative areas of use. We also may have classified some movements of deer as unusual because we did not know their complete history. For example, a female captured and marked as an adult may have dispersed to the area of capture as a yearling, but made occasional trips back to her natal area.

A variation of the yearlong resident pattern also was evident for some deer (Fig. 8.8). During 3 years, female 0476 displayed a pattern typical of residents and her annual PHR varied from 1.7-4.8 km^2. She occurred within the same area during 2 other years, but moved to auxiliary winter areas during 2 very severe winters (points B, winter 1977-78 and points C, winter 1978-79; Fig. 8.8). During most years and snow conditions, her normal winter area was at the northeast corner of her home range. During 1977-78, she did not move to auxiliary winter range until early February, after 2 months of deep snow. Subsequent snowstorms resulted in her movement

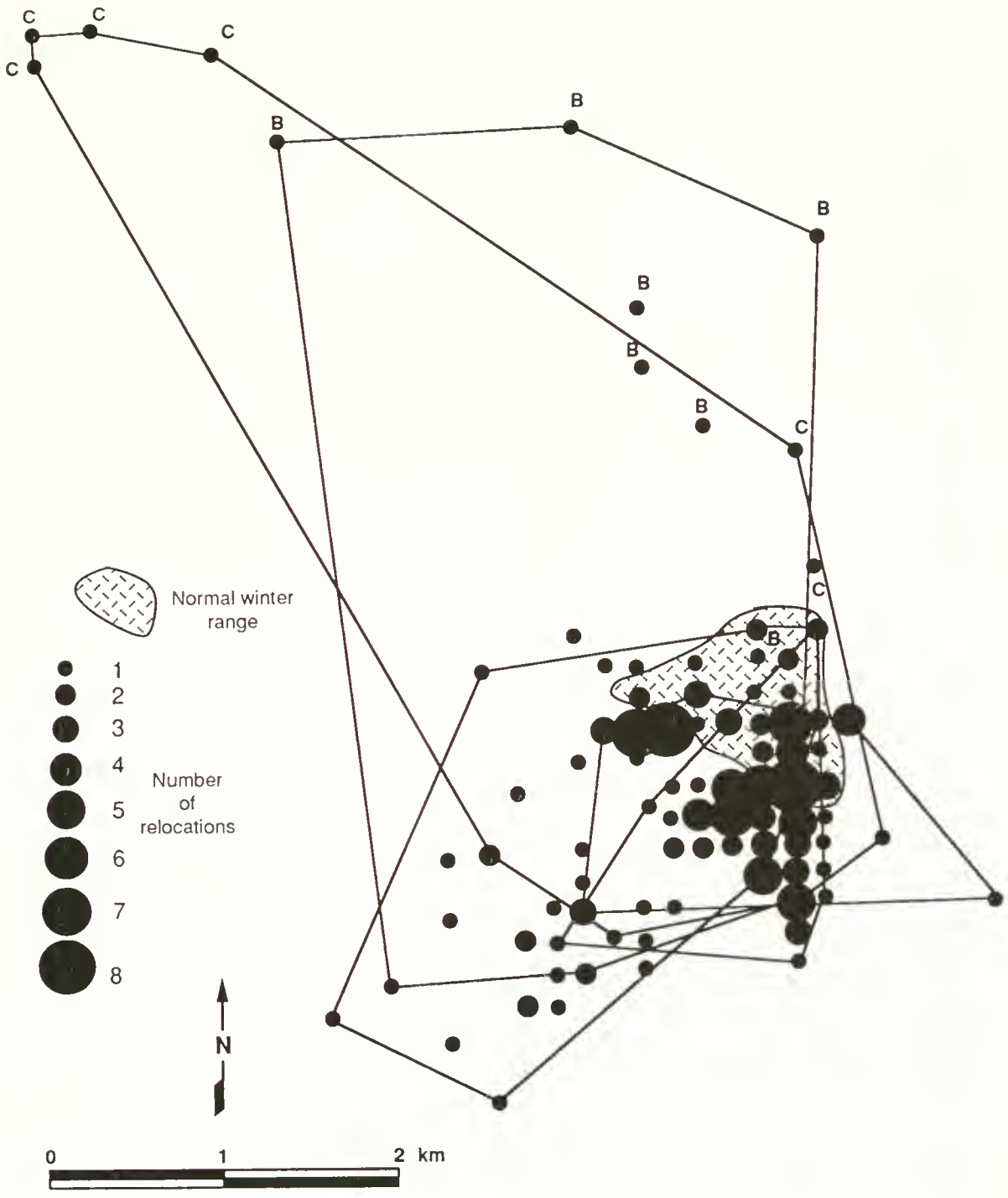


Figure 8.8. Annual home range perimeters (5 years), intensity of use plot, normal winter range, and auxiliary winter locations (B, 1977-78; C, 1978-79) for female 0476.

across a major drainage (Sand Creek) to a large complex of south- and north-facing slopes. She wandered throughout that complex during the remaining month of winter. During winter 1978-79, also very severe, she did not leave her normal winter area until late January, but when she did move, she immediately went to the last area she had used the previous winter and remained localized there for the remainder of winter.

During most years, female 0476 occupied a yearlong home range, but when snow depth exceeded 60 cm during 1977-78 and 1978-79, her normal winter range was not adequate. Snowdrifts from unusual north and east winds often covered the smaller south-facing slopes of her normal winter range. She finally moved to an area that contained south-facing slopes with twice the elevational gradient of those on her normal wintering area. South-facing slopes on the auxiliary winter area bordered on a large open drainage bottom, with the closest major ridge to block the sun during early and late portions of the day more than 1.5 km away. On her normal winter area, smaller south-facing slopes were bordered by ridges on the south less than 200 m away, effectively blocking sun from much of the south-facing slope except during mid-day.

The pattern of movements exhibited by this female during the severe winters of 1977-78 and 1978-79 indicated that she did not have an auxiliary winter range or that its location was a distant memory (she was a yearling during the previous severe winter of 1971-72). Her movements during winter 1977-78 indicated that she moved only when forced by extreme circumstances and then she did not go directly to an auxiliary winter range, but progressed through a series of more distant sites, apparently as the result of wandering movements. During winter 1978-79, however, once conditions became severe, she immediately moved to the best auxiliary winter range site she had encountered during her wanderings the previous winter. Other resident deer had similar patterns of movements during those severe winters. The speed and directness with which they moved to auxiliary winter range sites varied and may have depended upon their previous experience or that of the matriarch in their social group.

Female 0476, as the others profiled, spent most of her time in a much smaller area than indicated by PHR size (Fig. 8.8). A total of 64% of the relocations of female 0476 were within an area that was 4.2% of her life PHR and 13% of her life PHR that excluded relocations during severe winters. This deer did not need an area of 21.9 km^2 (total life PHR) to survive, but during some winters she did need to use areas 5 km from her normal home range.

The pattern of home range formation for resident female 3580 from birth until age 4 is shown in Fig. 8.9 (annual PHR 1-4). Annual PHR size varied from 3.1 to 5.4 km^2. The AAR was smallest during the year she was a fawn (0.5 km), largest when she was a yearling (1.0 km), and intermediate during the years she was 2 to 4-years-old. Although exploratory movements took place and some important areas of use expanded slightly northeast, 70% of all relocations after 12 months of age were within the boundaries of her first year home range. Fifty-six percent of all relocations during the 4 years were within an intensively used area of 0.5 km^2 that was 4% of her life PHR and 14.5% of her smallest annual PHR. Except during periods of deep snow when she moved to an area with larger south-facing slopes (Fig. 8.9), this female used the same areas during winter as during the rest of the year.

For female mule deer on the study area, the majority of which do not disperse from ancestral home ranges as yearlings, the area in which they spend their first year becomes a major portion of their adult home range (Fig. 8.9). During fawn-rearing periods, however, mother and daughter seldom use the same location at the same time (Fig. 7.12). Female fawns of migratory females became migratory as well, and used the same general summer and winter areas as their mothers; though the timing of movements between areas was often independent. The general home range size, shape, and pattern of use appeared to be the result of learning and tradition, but daily movements were most often independent, especially from May through early autumn.

Although the literature indicates that broad differences in habitat can alter home range characteristics, it is difficult to closely relate home range characteristics to habitat within one study area. We hypothesized that deer living in areas with large amounts of open area between islands of cover might have larger home ranges than those deer living in areas that included a lot of interconnected cover. If there were differences in home range size within our study area owing to varying habitat components, our gross analysis did not detect it. Nineteen summer home ranges were calculated for 9 resident adult females whose home range included or bordered on large amounts of sagebrush-grassland or pine-grassland cover types. Mean PHR for those deer was 3.11 km^2 and mean AAR was 0.86 km. Mean PHR for all resident adult females was 3.44 km^2 and mean AAR was 0.83 km.

As discussed earlier, habitat probably largely determined whether deer were migratory or resident, and thus affected home range size. Overlapping home ranges of 3 resident and 4

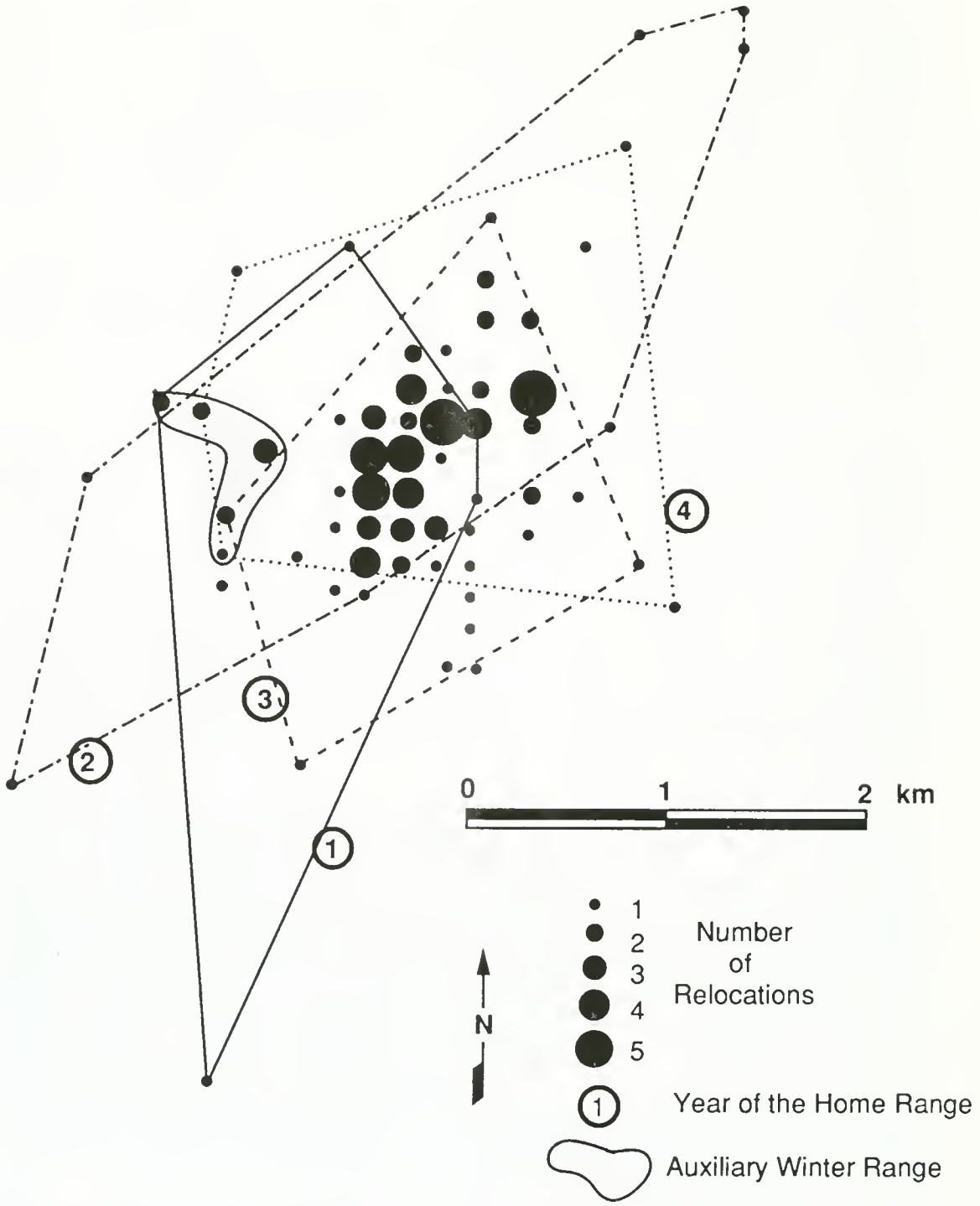


Figure 8.9. Annual home range perimeters of female 3580 from birth to age four. Intensity of use plot and auxiliary winter range location are included.

migratory females helped explain how habitat affected home range (Fig. 8.10). Polygon home range size for 3 resident females was much smaller than that of 4 migratory deer. There was no acceptable winter range adjacent to the spring-summer ranges of the 4 migratory deer, and they moved 4-6 km to other areas during autumn and winter. Three of the 4 migratory deer used the same areas during winter and the other used a different winter area (Fig. 8.10). Winter areas were less than 1 km from the center of the PHR of resident females.

We believe that "parturition territoriality" (Ozoga et al. 1982a) and the limited availability of quality wintering sites led to the establishment of the migratory movement pattern. Because not all deer that used the area included in Figure 8.10 were marked, total home range overlap could not be mapped. It is likely, however, that territoriality during parturition and the early post-partum period limited the number of females that could establish residence near areas suitable as winter range. As the population increased, parturition territories were established at increasing distances from high quality winter range.

Females establishing fawn-rearing territories at some distance from the winter range probably were fawns of females resident to winter range areas. After fawn rearing territories became less rigid during late summer and autumn, the younger females may have regrouped with their mothers and continued to use the same winter areas. As time passed and the older females died, the younger females continued to use separate summer and winter areas because of tradition and necessity rather than because of social ties. During mild winters, it was possible for deer to remain in the spring-summer range of females A, C, D, and E (Fig. 8.10). During winters with deep snow, however, it is unlikely that many deer, especially fawns, remaining in those spring-summer areas would survive. Over the long term, females that have spring-summer home ranges in areas of low relief near the prairie are unlikely to recruit many fawns (genes) or survive themselves if they do not maintain a migratory tradition.

The resident pattern is probably the natural pattern because it is less costly in terms of energy expenditure and exposure to hazards. However, when an area is near maximum fill, at high population levels, a migratory movement pattern must develop. Some deer establish a resident pattern in low relief habitat, especially during long, mild weather cycles, but they are those most likely to die during severe winters.

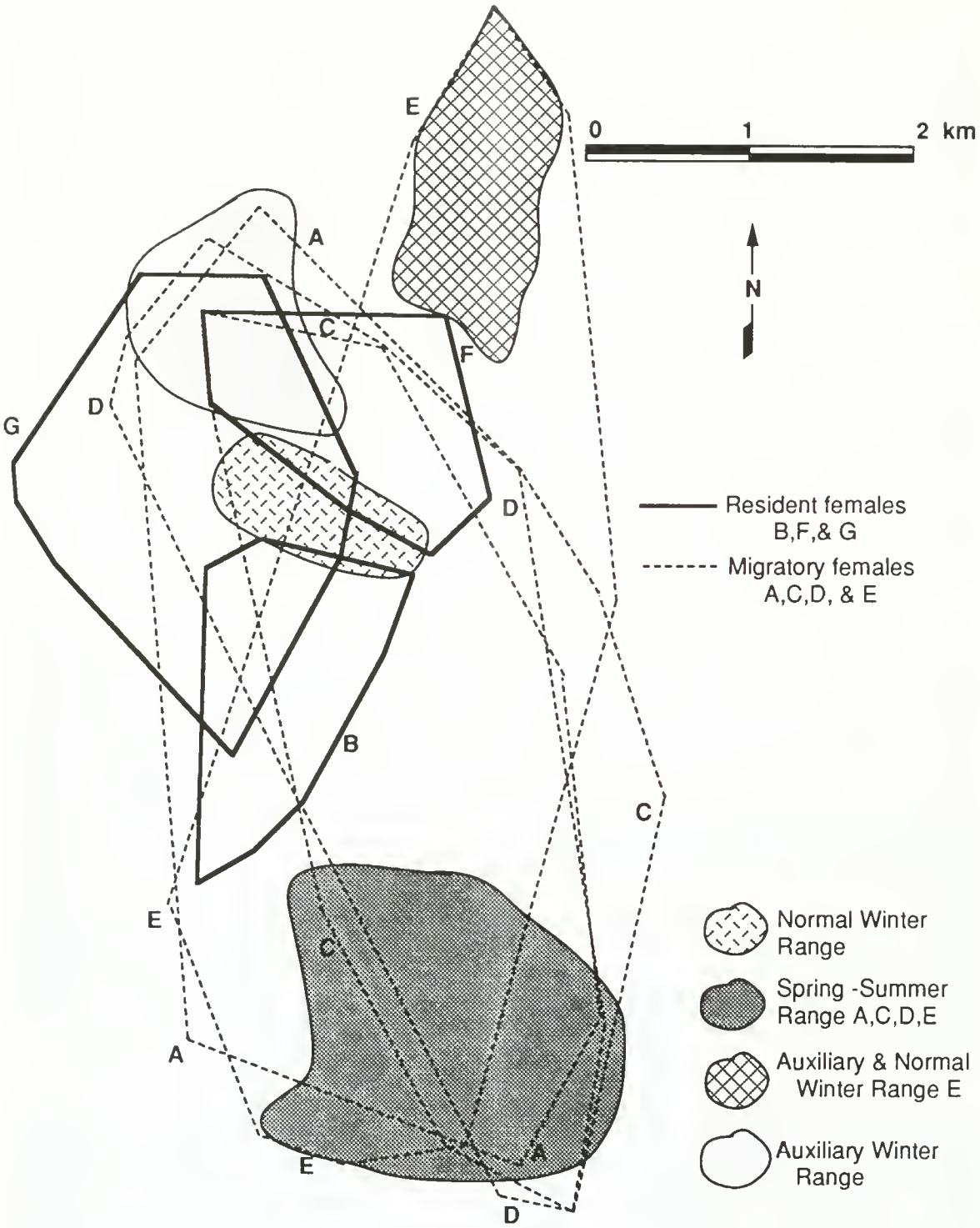


Figure 8.10. Life home range perimeters, summer, winter, and auxiliary winter range locations for three resident and four migratory females.

Some deer moved to new areas of use during autumn and remained near there during winter (Fig. 8.7). We believe that movements of autumn migrants may have been at least partially influenced by cattle grazing. The areas of low relief and more open cover types that those deer moved from were generally intensively used by cattle. The areas they moved to, while providing steep south-facing slopes and thermal cover on timbered north-facing slopes during winter, also provided advantages during autumn. The steeper terrain was less grazed by cattle and forage remained succulent longer on the more extensive north-facing slopes. As a special case, the autumn and winter ranges of females A, C, D, and E (Fig. 8.10), were within a "blind pocket" in the fencing system and received exceptionally light use by cattle. Coincidentally, the area they used during spring-summer may have been improved as spring range because of heavy use by cattle during summer and autumn. The lack of litter in those areas made early spring growth of grasses and forbs more available to deer.

Discussion

We identified 2 general types of movement patterns for adult females; resident and migratory. Within that framework, however, home range size and movement patterns were extremely variable, not only among deer and among seasons and years, but for the same deer among seasons and years. Much of this variation reflected seasonal and annual adaptation to fluctuations in environmental conditions. The form of these adaptations or adjustments depended upon the topographic, climatic, vegetational and land use characteristics of individual home ranges. Males generally had larger home ranges than females. Home range during summer was smaller for females with fawns than for those without fawns. Home range size of adult females was not affected by deer density or forage abundance, but summer home range size for fawns and thus parturition territory of adult females was smaller at higher densities.

A home range develops as the result of tradition and cumulative movements to satisfy daily requirements. Any successful home range strategy must result in procurement of enough quality forage, warm microsites during winter, escape terrain from predators, hiding and thermal cover, and other amenities to enable the deer to survive and successfully recruit young. Generally, the smallest area to supply all those amenities should be the most efficient home range size.

Initially, the matrilineal social structure of mule deer in this area provides the basis for home range formation by females. The mother aggressively breaks the social bond with her yearling daughter just prior to the birth of her new fawn(s). During most years, few yearling females disperse

from their natal range and although their mother does not tolerate their close presence during summer as long as her new fawn(s) survive, the yearling daughter maintains an overlapping home range with her mother. The yearling daughter does not use the same spot at the same time as her mother during this period but based on the learning and tradition established during her first year of life, continues to generally use the same home range as her mother. The yearling summer may also be characterized by exploratory movements beyond the boundaries of the mother's home range. Although those movements may eventually lead to small shifts in intensity of use patterns, colonization of new sites is often unsuccessful because the yearling encounters the parturition territories of other females and is chased from those.

During autumn, or earlier if the mother's new fawns die, the yearling usually rejoins the mother and a matrilineal group is formed. Apparently, the resources within any home range are sufficient to support more than 1 female and the formation of matrilineal groups results in sharing of resources by relatives rather than unrelated deer. Any possible diminution of resources for the matriarch and her current fawns must be more than balanced by genetic advantages of kin-selection apparent in sharing with older daughters and granddaughters rather than allowing unrelated females to preempt portions of her home range. The daughter's chances for reproductive success are enhanced by her use of known resources on a successfully established home range. Dispersal, especially during periods of mid-high population density, could only result in establishment of a home range in marginal areas not yet used by successful females. Resources are marginal on these areas and their location must be learned by trial and error, exposing the disperser to greater peril from the weather, predators, and accidents. Those considerations may explain why most dispersal we observed by yearling females was at pre-saturation densities, when relatively better habitat was still unfilled.

Once a home range is established, daily and seasonal movements within that area appear to be governed by actions that enhance the comfort and survival chances of the deer. A question to be answered by an examination of movements is: What types of areas best provide for the comfort and survival of deer? Although detailed analysis related to that question was not done, the available data did result in some obvious conclusions. Movements of deer during late summer and autumn indicated that the changing availability of high quality, succulent forage motivated those movements. The deer that shifted their areas of use during late summer and autumn most often moved from areas of low topographic diversity to areas that contained more topographic diversity and a wider variety of microsites. Broad north-facing slopes and the attendant

smaller drainage bottoms provided succulent forage longer than did other areas. Forbs and shrubs under the Douglas-fir canopy on most north-facing slopes not only were subject to less evapotranspiration stress during the heat of summer, but were protected from the earliest killing frosts of autumn by a temperature-moderating effect of forest canopy. Those deer living adjacent to the Missouri River bottom made more use of the river riparian type during autumn for similar reasons.

During winter, forage was less of a driving force in determining movements and habitat use. In the northern United States and on this area, most of the forage available to deer during winter is of only maintenance quality or poorer (Bucsis 1974, Short et al. 1974, Mautz et al. 1976, Wallmo et al. 1977, Mautz 1978). Plant species making up the bulk of the winter diet on this area (big sagebrush and Rocky Mountain juniper) are abundant and ubiquitous. During mild or "normal" winters, deer can find adequate quantities of most winter forage almost everywhere. However, rabbitbrush, a preferred species, was primarily available at the edge of ridges in the ecotones between sagebrush and pine and Douglas fir types and when snow depth was greater than about 45 cm, most rabbitbrush was unavailable.

Although snow depth was reduced on the south- and north-facing slopes deer moved to during severe winters, forage availability did not appear to be the factor governing those movements. The south-facing slopes on the severe winter areas were usually either the pine-juniper-shale or greasewood and shale-longleaf sage vegetation types. Those types were the poorest of all types in forage quantity and quality (Tables 3.2 and 3.3). Use of the auxiliary winter areas provided deer with ease of movement and escape from predators, warm sites on sunny days on the south-facing slopes and relatively warmer sites on the timbered north-facing slopes at night and during cold, windy days.

During spring, deer made the greatest use of the open sagebrush-grassland type and least use of the dense Douglas fir types. Such use was related to the greater availability of new green forbs and grasses in the open types. It required movement of only 100-200 m to open areas rather than major movements to entirely new areas of use.

The home range of males should also contain adequate resources for survival, but the requirements of males differ from those of females (Verme 1988). Our data indicated that males occupied lower quality habitat than productive females did, at least during summer and early autumn (Chapter 9). Data on social structure, distribution, movements, and habitat use indicated that males, especially during the fawn-rearing period, spend most of their time on sites not occupied by

productive females. Females with fawns aggressively chased males, as well as other adults, during the fawn-rearing period and most mature males were distributed in aggregations away from productive females during summer and early autumn. Additionally, data from marked deer indicated that most mature males and females were not associated during winter and spring.

The relatively larger home range size of males compared to females is probably explained by 2 factors; breeding strategy and movement during the rest of the year among widely separated patches of habitat not occupied by many productive females. The greatest portion of the explanation for larger home range size of males may be related to breeding strategy. Because males do not face lactation stress during summer, their nutritional requirements during summer are probably less than that for productive females. They also do not require habitat with adequate hiding cover from predators that females protecting young fawns require. Rather than concentrate resources on raising a single litter of fawns per year, the reproductive strategy of the mature male is to have access to and breed as many females as possible each breeding season. A large home range results in access to more females (Fig. 8.11).

Many other unmarked males and females used the area presented in Figure 8.11, so that plot does not represent the home range of one male and all of his exclusively available females. The data do illustrate the relative degree of access of the male to different females compared to the potential for female interaction with each other. The home range of the male encompassed at least 3 subpopulations of females that had little or no interaction with each other. Familiarity with a large area provided the male with maximum potential breeding opportunities. Relocations made during the breeding season (Fig. 8.11) indicated that he moved throughout his entire home range during that period.

Home range size, shape, and pattern of use for both females and males evolved as that which when used, resulted in the greatest number of recruited offspring. Females probably use the smallest home range that supplies all their needs. The matrilineal social structure, parturition territoriality, and changes in deer density all interact to determine whether a particular female can establish a home range that is optimal or marginal in its amenities. Males attempt to have access to many females during the breeding season, while using areas where they do not compete with their offspring for forage or space during the rest of the year.

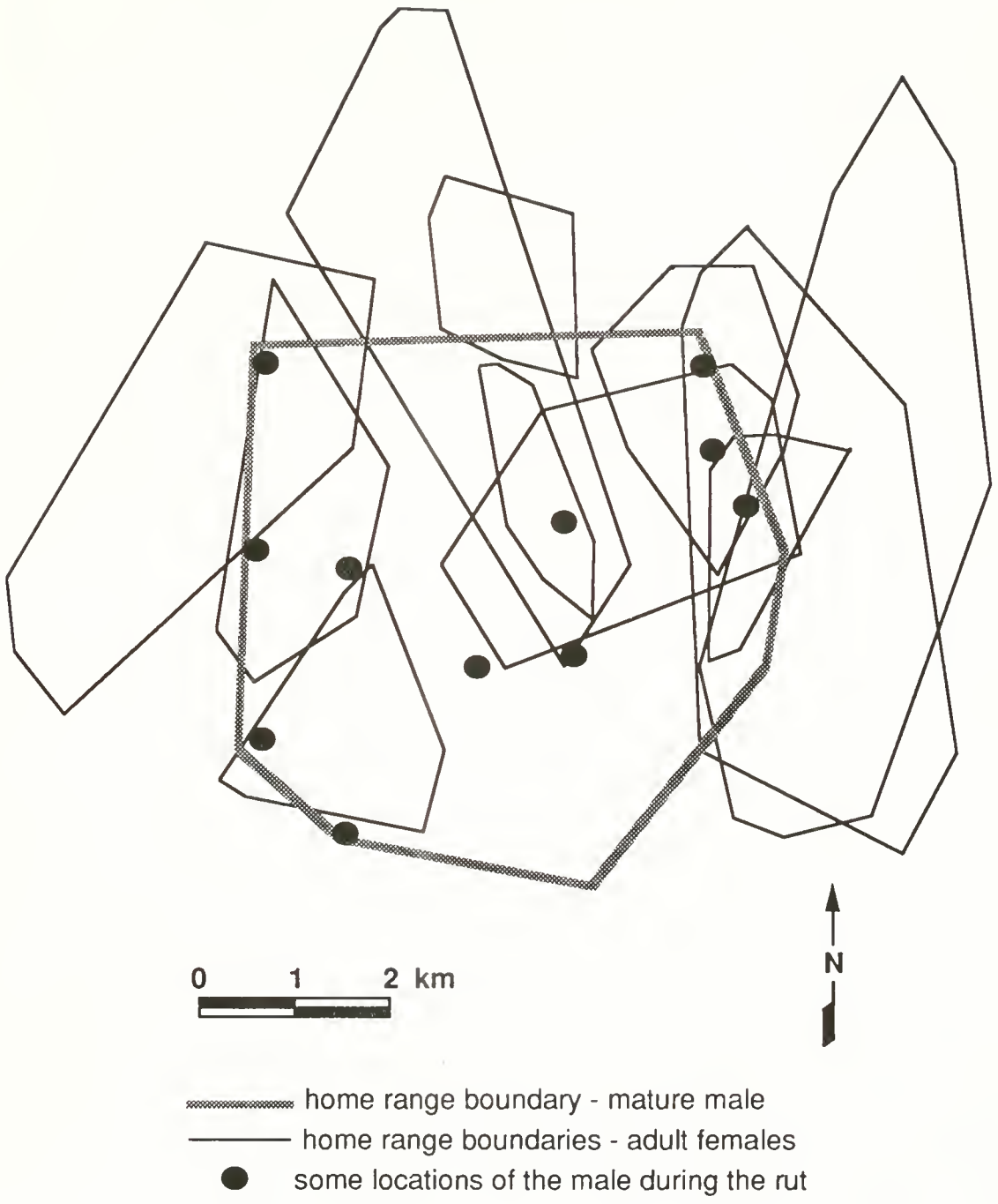


Figure 8.11. Relative distribution of home range perimeters for a mature male and eleven adult females.

Although often considered a species/population parameter, our data indicate home range size and shape as well as movement patterns are influenced to a large degree by individuality. They reflect an individuals attempt to effectively utilize the fixed habitat base in an area and survive under prevailing environmental conditions and fluctuations.

CHAPTER 9

HABITAT USE AND INTERSPECIFIC RELATIONS

Food Habits

Food habits of mule deer on and adjacent to the study area were emphasized in earlier work by Mackie (1970), Knowles (1975), and Komberec (1976). During 1976-1986, we obtained additional information by collecting rumen samples from hunter-killed deer during late October through November each year, as well as from coyote-killed deer, trapping casualties, road-killed deer, or deer deliberately collected for study. The following discussion generally summarizes our knowledge of food habits from both the earlier published reports and the additional information.

On an annual basis, shrubs comprised 62%, forbs 33%, and grasses 5% of the mule deer diet during 1960-1964. Shrubs comprised 50% or more of the diet during August through March, and averaged 36% of the diet during May through July, their period of lowest use (Figure 9.1). Peak use of shrubs occurred during December and January (90%+). Forbs comprised one-third or more of the diet during April through September. Forb use was highest during May, June, and July, when it comprised 60-70% of the diet of mule deer. Lowest use of forbs occurred in December and January, coinciding with the greatest use of shrubs. Use of grasses was relatively minor, but peaks occurred during October and November of some years and late March through April in all years.

Seasonal Patterns

Summer

Forbs comprised 45-75% of the summer diet of mule deer, averaging slightly over 50% (Mackie 1970, Knowles 1975). Yellow sweetclover was the major forb species used, comprising 36-59% of the diet. A variety of other forbs were also eaten, usually in minor amounts. The shrub, fragrant sumac, was the second-most important forage species during summer, comprising 10-36% of the diet. Both Mackie (1970) and Knowles (1975) noted that use of fragrant sumac increased as the abundance and succulence of yellow sweetclover decreased. During summer, use of fragrant sumac was primarily confined to leaves and buds. Other shrubs, including snowberry, rose, and chokecherry received increasing use as summer progressed. Grasses received minor, incidental use during summer. When sweetclover was scarce or absent, use of other forbs increased to a small degree, but most of the lack of yellow sweetclover was made up by increased use of fragrant sumac, snowberry, rose, and chokecherry.

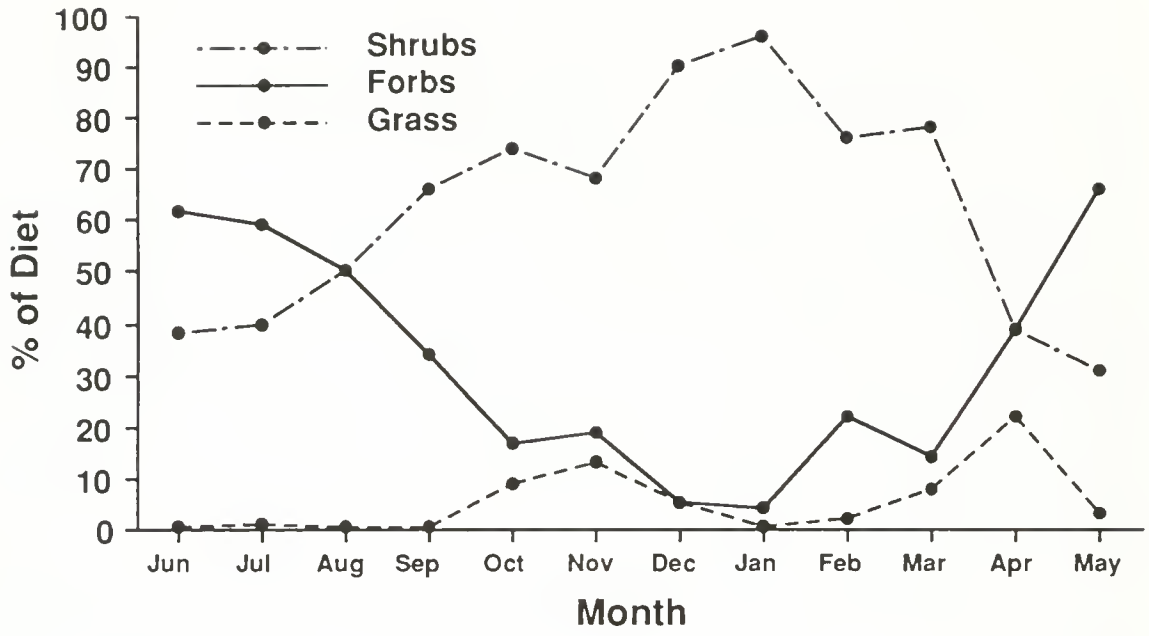


Figure 9.1. Yearlong trend in mule deer use of browse, forbs, and grasses in the Missouri River Breaks, Montana, 1960-1964.

Autumn

General comments about forage use during autumn from Mackie (1970) and Knowles (1975) were supplemented by data from late autumn for 1976-1986 (Table 9.1). The species of forage used was highly variable during autumn, but use of shrubs generally exceeded use of forbs. Exceptions occurred when first-year growth of yellow sweetclover was available and remained succulent into autumn (1978, Table 9.1). Sweetclover was important as long as it remained green, even into winter. Use of grasses during autumn was also variable among years and considerable use of Sandberg bluegrass was recorded during autumn 1977, 1985, and 1986 (30-48% of diet). This increased use of grasses resulted from autumn "green-ups" that occurred after substantial late summer-early autumn rains. Autumn use of green grasses also occurred during 1961 and 1962 (Mackie 1970). Relatively heavy use of grasses (14%) also occurred during very dry autumns (1980 and 1984). The majority of that use was of dry grass, apparently eaten incidentally in attempts to eat the few remaining green leaves.

The major forage species used during autumn of most years was rabbitbrush, primarily rubber rabbitbrush, but also green rabbitbrush. Use of rabbitbrush was seldom great prior to about the first part of October, when flowering was finished (Knowles 1975). Rabbitbrush not the most important forage species only during autumns when sweetclover remained green

Table 9.1. Major food species used by mule deer during late October through November, 1976-1986, as determined by rumen analysis, Missouri River Breaks, Montana.

Species	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1976-86
	4[a]	11	8	10	15	14	10	10	9	5	10	106
Grasses	tr[b]/25	37/100[c]	tr/13	tr/20	14/67	5/50	2/60	10/70	14/67	48/100	30/80	15/59
Green grass	tr/25	35/100	tr/13	tr/20	1/67	1/50	tr/60	5/70	4/67	32/100	22/80	9/59
Dry grass	tr/25	2/100	tr/13	tr/20	13/67	4/50	2/60	5/70	10/67	16/100	7/80	6/59
Forbs	5/75	3/64	55/100	30/90	5/53	7/57	11/60	4/50	10/67	28/100	23/90	16/67
Melilotus officionalis		tr/9	50/100	27/70		6/50	7/60	1/10		13/40	tr/20	9/32
Shrubs	94/100	60/100	45/100	69/100	81/100	88/100	87/100	86/100	76/100	24/100	47/100	69/100
Artemisia tridentata					8/33	tr/29		9/40	1/22		tr/30	2/17
Chrysothamnus spp.	57/100	20/82	tr/13	24/90	24/93	47/100	37/100	40/90	37/100	4/60	14/80	28/85
Juniperus scopulorum	tr/25	2/36		2/40	3/67	5/64	12/100	17/80	13/78	5/80	7/60	6/59
Rhus aromatica	tr/25		tr/25	1/50	11/60	1/21	5/20	tr/10	1/11		1/20	2/24
Rosa spp.	25/100	1/82	4/88	15/90	4/80	2/64	3/70	1/40	1/33	3/80	3/40	6/68
Symphorocarpos spp.	10/100	37/100	41/100	27/90	22/93	32/93	28/90	12/70	8/78	12/80	10/80	22/89

[a] number of rumens
[b] tr - trace = < 0.5%
[c] % volume/ % frequency of occurrence

and/or a "green-up" of grasses occurred. Snowberry ranked second in both use and occurrence among species used during autumn. Its use was especially heavy during good fruit-bearing years when the berries were probably a source of high energy. Rose, while not usually a major food item, was used consistently and was also most heavily used when rose hips, possibly high in energy (Welch and Andrus 1977), were abundant. Use of fragrant sumac was usually negligible after leafdrop in September. Autumn use of Rocky Mountain juniper and big sagebrush was relatively minor, but was more important when sweetclover or green grasses were not available.

Winter

More than 80% of the diet during winter consisted of shrubs during most years. Use of forbs was generally low except during periods of deep snow, when desiccated forbs, protruding above the snow, were eaten, and during warm, snow-free periods, when some forbs "greened up" on south-facing slopes. Grasses were generally used only during late March as new growth started.

Forage use during winter usually depended upon 2 major factors: snow depth and forage use during autumn. Big sagebrush and Rocky Mountain juniper were major forage species during winter in either case. Rabbitbrush was preferred and heavily used whenever it was available, but deep snow reduced both availability and use. Essentially, all current annual growth of rabbitbrush was utilized each year. When green forage was available during autumn and use of rabbitbrush was reduced, much of the use of rabbitbrush was delayed until early winter, when it received heavy use. Use of rabbitbrush then declined through winter as use reduced availability. Rabbitbrush may be depleted earlier in winters with high deer populations than during winters with low populations. Approximately 28% of the diet was rabbitbrush during February 1977 (470 deer), 20% during February 1980 and 1981 (1020-1030 deer), and only a trace during February 1984 (1545 deer). However, the latter periods also coincided with dry conditions, leading to heavy autumn use of rabbitbrush.

There was more than 30 cm of snow on the ground for 97 and 112 days and more than 45 cm of snow on the ground for 85 and 96 days during winters 1977-78 and 1978-79, respectively. Winter 1981-82 was less severe than either 1977-78 or 1978-79, nevertheless, snow depth was 23 cm or more for 58 days. Rabbitbrush was essentially unavailable those winters and received little use regardless of population level (Table 9.2). Fragrant sumac was also largely unavailable and was used much less than in more open winters. Rocky mountain juniper and big sagebrush were heavily used and very heavy use

Table 9.2. Major food species used by mule deer, late December through early March, 1976-1977 through 1981-1982, as determined by rumen analysis, Missouri River Breaks, Montana.

	1976-77	1977-78[a]	1978-79[a]	1979-80	1980-81	1981-82[a]	Winters of deep snow	Winters of little snow
Species	9[b]	5	5	6	7	4	14	22
Grasses	tr[c]/44			tr/17	tr/29	19/25		
Forbs	9/44[d]	1/20	15/80	20/83	tr/5	7/100		
Artemisia longifolia	8/44		2/60	9/50				
Melilotus officionalis	tr/11		tr/20	11/67				
Shrubs	91/100	99/100	85/100	80/100	99/100	74/75		
Artemisia tridentata	13/89	19/100	22/100	7/50	26/100	15/75	19/93	15/82
Chrysothamnus spp.	37/100	7/20	2/20	24/67	25/67		3/14	29/82
Juniperus scopulorum	18/100	17/100	29/100	9/100	21/100	36/75	27/93	16/100
Pinus ponderosa		33/100	16/60	1/17	1/29	17/75	22/79	1/14
Rhus aromatica	8/78	12/80	5/40	27/83	23/86	1/25	6/50	19/82

[a] Winter of deep snow
[b] Number of rumens
[c] tr = trace = < 0.5%
[d] % volume / % frequency of occurrence

was also made of ponderosa pine needles. Despite this, mortality, especially of adults, was relatively light during those winters and fawn mortality was less than during some milder winters.

Overall, it appeared that rabbitbrush was the preferred winter forage and that use of big sagebrush and Rocky Mountain juniper increased only as a result of declining availability. Similar conclusions were made by Dusek (1975) for mule deer north of our study area. These conclusions may be consistent with Nudds (1980) hypothesis that deer are forage generalists when winter conditions are severe.

Spring

Use of forbs increased throughout spring and reached an annual peak during May. Shrub use usually declined by late March when "green-up" of new growth was initiated, though in some years "green-up" did not begin until early April. Use of grasses increased when new growth was initiated and reached an annual peak of around 20% of the diet in April, declining thereafter as forbs became more abundant. The major grass species used during spring was Sandberg bluegrass. Important forbs used during spring were bastard toad flax (*Comandra umbellatum*), wild onion (*Allium textile*), oyster plant (*Tragopogon dubius*), wild parsley (*Musineon divaricatum*), lomatium (*Lomatium foeniculaceum*), and American vetch (*Vicia americana*).

Discussion

Green, succulent forage was preferred whenever it occurred. When sufficient late summer and/or autumn rainfall and relatively warm autumn temperatures resulted in maintenance of succulence of forbs or promoted regrowth of forbs and grasses, use of normal autumn browse species was delayed. These autumn browse species, especially rubber rabbitbrush, were then available for longer periods into winter. Heavy dependence by mule deer on Rocky Mountain juniper and big sagebrush was delayed further into winter. An autumn green-up prolonged the period of good to adequate nutrition not only through autumn, but into winter. Conversely, drought led to earlier maturation and desiccation of all herbage and in turn to heavy utilization of preferred browse, decreasing its availability during winter. Generally, a shorter winter season occurred on our study area than in most mountainous areas of the Rocky Mountains. Regrowth often began by late March although it was sometimes delayed until mid-April.

During occasional winters of deep, continuous snow cover, much of the area was not inhabitable by deer. Many deer using

the southern portion of the study area migrated northward to areas of greater relief with steep south-facing slopes. Those areas were characteristically poor in forage resources, regardless of deer numbers. The most preferred winter forage, rubber rabbitbrush, was covered by deep snow and was usually absent on the steeper areas where deer are forced to winter.

Paradoxically, effectively long winters (periods of negative energy balance), were often the result of hot dry springs, summers and autumns rather than deep snow and cold temperature during the calendar months of winter. Dry conditions during spring through autumn resulted in earlier than normal and heavy use of rubber rabbitbrush and snowberry which led to unseasonably early dependence on big sagebrush and Rocky Mountain juniper.

The nutritional quality of the mule deer diet was influenced at least as much by the density-independent factor of climate as by the number of deer competing for forage. Weather certainly acted with more regularity than intraspecific competition on the nutritional quality of the deer's diet.

General Patterns of Habitat Use

Earlier studies (Mackie 1970, Knowles 1975, Komberec 1976) defined general patterns of habitat use by mule deer. Therefore, data obtained during 1976-1984 were primarily used to evaluate and refine previous conclusions about habitat selection and habitat factors influencing population ecology of deer in riverbreaks habitat. Aerial surveys ensuring complete coverage of the study area during July, September or October, December or January, and March or April provided the most complete data for analysis. Locations from individual surveys, recorded as the mid-point of 3.2 ha cells, were compiled seasonally and interpreted to represent habitat use and selection during summer, autumn, winter, and early spring.

A "block analysis" (Porter and Church 1987, Wood 1987) was employed. This involved (1) compiling numbers of deer observed during aerial surveys within 28.8-ha blocks to determine relative seasonal density or intensity of use of each of the 953 blocks on the area and (2) relating those data to various habitat attributes measured within each block. The latter included the kind and amount of each vegetation cover type, the number of different cover types, the number of different patches of cover, a topographic relief index, and distance to free water during wet and dry years.

Habitat parameters were measured from a vegetation cover type map developed from aerial photographs and ground-truthing

as overlays to orthophoto and topographic quadrangle maps of the study area. The kinds and amounts of vegetation cover types in each 28.8-ha block were measured by superimposing a dot grid of 25 regularly spaced points on each block and recording the type under each dot. Each cover type was assigned a value from 0 to 25 in each block, weighing its relative importance. The number of different cover patches was counted as the number of discrete units of all types in the block. The topographic index was determined by counting the number of contour lines intersected by 1 line drawn horizontally and 1 drawn vertically through the center of each block. Each block was then assigned to 1 of 4 TOPOINDEX categories: 1 = 0-69 m relief/km ($\bar{X}$ = 34 m/km); 2 = 70-149 m/km ($\bar{X}$ = 114 m/km); 3 = 150-230 m/km ($\bar{X}$ = 195 m/km); and 4 = 231-321 m/km ($\bar{X}$ = 275 m/km). Distance to water was measured from the center of the block to the nearest water source known to exist seasonally during wet and dry years within one of 5 distance classes: 1 = 0-0.402 km; 2 = 0.403 - 0.806 km; 3 = 0.806 - 1.61 km; 4 = 1.62 - 2.41 km; and 5 = > 2.41 km.

Use and Selection of Vegetation Cover Types

Mule deer used blocks containing forested cover types more than expected during all seasons (X^2 = 129.9 to 550.4, 1 df, $P < 0.005$). Forest types comprised 51.5% of the study area and 63.4%, 61.4%, 66.9%, and 60.9% of blocks used by deer during summer, autumn, winter, and spring, respectively. Deer use of forested types was greater during winter than all other seasons (X^2 = 8.41 to 36.7, 1 df, $P < 0.005$). Deer also used forested types proportionately more during summer than during spring (X^2 = 4.49, 1 df, $P = 0.04$).

Data concerning relative use of individual vegetation cover types by season (Table 9.3) are presented as relative risk-odds ratios (Everitt 1977), which were used as a preference index. Values greater than 1.00 indicated that more deer than expected ($P < 0.05$) used blocks containing a particular type. The higher the value, the more the apparent selection. Values less than 1.00 indicated that fewer deer than expected ($P < 0.05$) used blocks containing that type. Where no value is listed, deer use was not significantly different from that expected based on relative availability.

Mule deer use of specific vegetation cover types differed seasonally (Table 9.3; X^2 = 378.76, 60 df, $P < 0.0001$). Blocks used by deer during summer contained more burned Douglas fir-juniper type than expected. They also used blocks containing moderate and open density classes of the Douglas fir-juniper and pine-juniper-shale types, and the shale-longleaf sage and grassy bottom types more than expected. Conversely, blocks where the sagebrush-grassland,

Table 9.3. Relative risk ratios for seasonal mule deer use of vegetation cover types. Values > 1.00 indicate selection for that type, values < 1.00 indicate avoidance, blanks in Table indicate use not significantly different than expected.

Vegetation Cover Type	Summer	Autumn	Winter	Spring	Year-long
Douglas fir-Juniper-moderate	1.48		1.46	1.34	1.37
Douglas fir-Juniper-open	1.43	1.58	1.88		1.52
Douglas fir-Juniper-scattered		2.62	1.62	0.59	1.46
Douglas fir-Juniper-burned	1.84	2.00	1.98	1.29	1.76
Pine-Juniper-Shale-moderate					
Pine-Juniper-Shale-open	1.40		1.42	1.38	1.33
Pine-Juniper-Shale-scattered	1.68	1.67	1.46	1.55	1.56
Pine-Fir-Juniper-moderate					
Pine-Fir-Juniper-open		1.81			1.27
Pine-Fir-Juniper-scattered					
Pine-Fir-Juniper-burned			1.78		1.68
Pine-Juniper-Grass-moderate		0.76		1.28	
Pine-Juniper-Grass-open			1.18		
Pine-Juniper-Grass-scattered		1.41	1.20	1.50	0.32
Pine-Juniper-Grass-burned					
River Riparian	0.06	0.42	0.14	0.03	0.15
Sagebrush-Grassland	0.59	0.55	0.48	0.73	0.58
Shale-Longleaf Sage	1.36	1.52	1.33		1.24
Greasewood	0.41	0.64	0.70	0.52	0.59
Silver Sagebrush		0.15	0.25	0.40	0.28
Grassy Bottoms	1.31				

greasewood, and river riparian types predominated were used less than expected during summer.

The Douglas fir-juniper and pine-juniper-shale types were often closely associated on adjacent north- and south-facing slopes such that the block method of analysis gave weight to both types even if one was preferred more than the other. Riley and Dood (1984) reported that the Douglas fir-juniper type was used proportionately more by mule deer fawns than the pine-juniper-shale type during summer. Overall, deer use was more widely distributed among types (i.e., there was less negative selection or avoidance of types) during summer than any other season.

Deer use of blocks containing the Douglas fir-juniper types remained high relative to other types during autumn, but overall use of blocks containing the pine-juniper-shale types declined from summer. The 2 Douglas fir types with the least overhead cover received the greatest use. Also, the scattered density pine-juniper-grass type received proportionately greater usage than the more dense pine-juniper-grass types. The river riparian type received more use during autumn than other seasons, but use remained less than expected based on availability.

During winter, deer selected for a variety of types, although Douglas fir-juniper types received their highest combined use of any season. Blocks containing the Douglas fir-juniper types received their lowest seasonal use during spring, and fewer deer than expected were observed in association with the scattered density Douglas fir-juniper cover type. The scattered density pine-juniper-shale and scattered density pine-juniper-grass cover types were the most selected types during spring. The sagebrush-grassland type, although not selected, received its greatest use during spring as influenced by the availability of forbs in that type (Table 3.3).

On a yearlong basis, deer were more closely associated with and apparently showed more selection for Douglas fir types, collectively, than for any other vegetation types on the area. Among cover types, the burned Douglas fir-juniper type received the greatest use relative to availability. The pine-juniper-shale vegetation type ranked second, but this may have been due at least partially to its close topographic association with the Douglas fir types and the method of analysis.

Any assessment of habitat selection based on observed use relative to availability is subject to possible shortcomings that must be addressed to place results in perspective and avoid false conclusions. The block analysis, in common with

several other methods of quantifying habitat selection, assumed that all vegetation cover types were equally available to all deer on the study area. That assumption was not met. For example, the Douglas fir types were distributed primarily on the western 60% of the area, where all other types also occurred. Deer on the eastern portion did not have the option of using fir, but had to choose among pine-juniper and other apparently less selected or preferred types. Because of this, the fir types probably were even more preferred and selected for than indicated by our analysis.

Distributional biases also were apparent in the relatively low selection indicated for other types, especially the river riparian and sagebrush-grassland types. The former was usually available only to deer ranging within about 3 km of the northern boundary of the area and could be entered only from one direction. Although our analysis indicated the river riparian type was used less than expected based on availability, general observations and movements of marked deer suggested it received relatively heavy use at least during autumn, by deer whose home ranges included some river bottomland.

Our analysis also indicated that the sagebrush-grassland type was not preferred during any season, whereas Mackie (1970) showed heavy and apparently preferential use of the type, especially during winter and spring. This type covered more of the study area than any other vegetation type. It occurred throughout, interspersed among forested and other types and as large vegetationally homogeneous blocks on major ridgetops and along the southern and southwestern fringes. Lacking diversity, such large blocks were not attractive to and received little use by deer. Further analysis showed that more deer than expected were observed in blocks containing 1% to 49% aerial coverage of sagebrush-grassland, and fewer than expected ($P < 0.0001$) occurred only in blocks containing more than 75% coverage (Fig. 9.2). This indicated that, although large blocks of the type were avoided, small patches interspersed with forested types were important to deer. This was especially true during spring green-up when general observations and data from earlier studies (Mackie 1970) indicated that a majority of the deer observed feeding were in sagebrush-grasslands.

In reporting earlier studies on habitat use by mule deer on the study area, Mackie (1970) noted that observability bias probably resulted in underestimates of deer use and the relative importance of the timbered pine-juniper and Douglas fir-juniper vegetation types as compared with open types such as sagebrush-grassland. We compared relative use of major vegetation types as determined by observations along vehicle routes during 1960-1964, by direct recording of vegetation

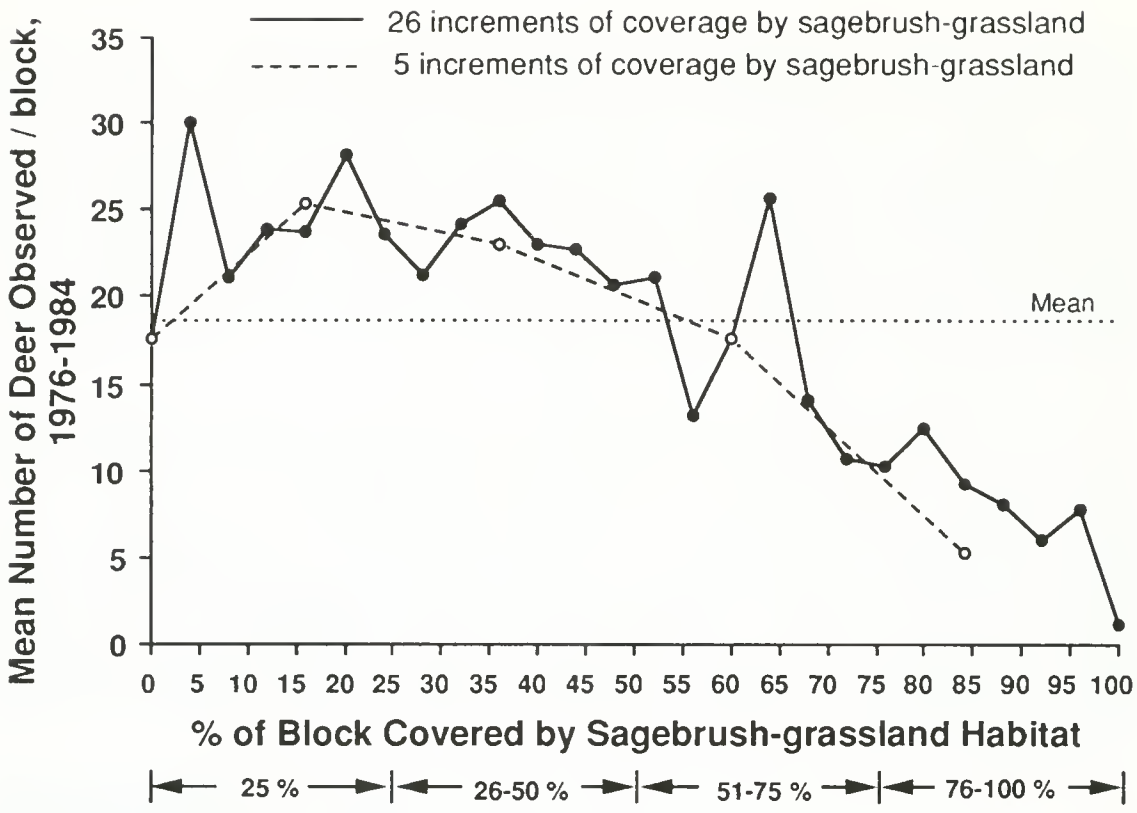


Figure 9.2. Use of sagebrush grassland type by mule deer in relation to amount of that type per 28.5 ha block.

types in which mule deer were observed during aerial surveys from July 1978 through April 1980, and block analysis of all aerial observations during 1976-1984 (Table 9.4).

All 3 methods showed similar use of the pine-juniper types, but use of Douglas fir-juniper types was higher and use of sagebrush-grassland was lower based on direct aerial observations and aerial observations submitted to block analysis than determined by observations along vehicle routes. All 3 methods also indicated that use of sagebrush-grassland was highest and use of Douglas fir-juniper types was lowest during spring. However, both direct aerial observations and the block analysis indicated the highest seasonal use of Douglas fir-juniper types occurred in winter when use as determined by vehicle routes was lowest. Observability differences between timbered and open habitats for vehicle routes and aerial observations must have been important, but some of this difference might have been influenced by winter severity. Approximately 54% of all mule deer observed from the air during the severe 1978-79 winter were in Douglas fir-juniper types compared to only 26% during the relatively mild 1979-80 winter. All winters during 1960-1964 were mild and

Table 9.4. Seasonal percentage use of vegetation type by mule deer, compared for three methods of observation and analysis.

Vegetation Type	Method	Season			
		Summer	Fall	Winter	Spring
Sagebrush-Grassland	Vehicle Routes	29	42	56	70
	Aerial Observations	7	5	9	41
	Block Analysis	26	25	23	31
Pine-Juniper	Vehicle Routes	48	33	32	21
	Aerial Observations	58	52	47	46
	Block Analysis	40	38	41	42
Douglas fir-Juniper	Vehicle Routes	11	10	2	1
	Aerial Observations	19	29	39	7
	Block Analysis	20	18	22	16
All Others	Vehicle Routes	12	15	10	8
	Aerial Observations	16	14	5	6
	Block Analysis	14	19	14	11

snow-free. Overall, the comparison indicated that our use of aerial survey data greatly reduced bias due to differential observability of deer in different vegetation types. It also confirmed Mackie's (1970: p. 33) suggestion that overall use of forested types was much more intensive than observations indicated and that relative use of sagebrush-grassland and other open types was minor, especially during summer and autumn.

Influence of Vegetational Diversity on Habitat Use

Both the number of different cover types and the number of cover polygons per block were considered indicative of habitat diversity. Amount of "edge" within blocks increased with number of cover types, while both edge and interspersion increased with the number of cover polygons; i.e., a block containing 2 polygons of each of 2 vegetation cover types (4 cover units) was considered more diverse than a block containing 1 polygon each of 3 different types (3 cover units).

Deer were not distributed randomly in proportion to the number of cover types available per block during any season (summer: $X^2 = 582.9$, 5 df, $P < 0.00001$; autumn: $X^2 = 642.1$, 5 df, $P < 0.00001$; winter: $X^2 = 1042.0$, 5 df, $P < 0.00001$; spring: $X^2 = 621.1$, 5 df, $P < 0.00001$). Fewer deer than expected were observed in blocks containing 1 or 2 cover types (Fig. 9.3), while blocks containing 3 cover types were used as

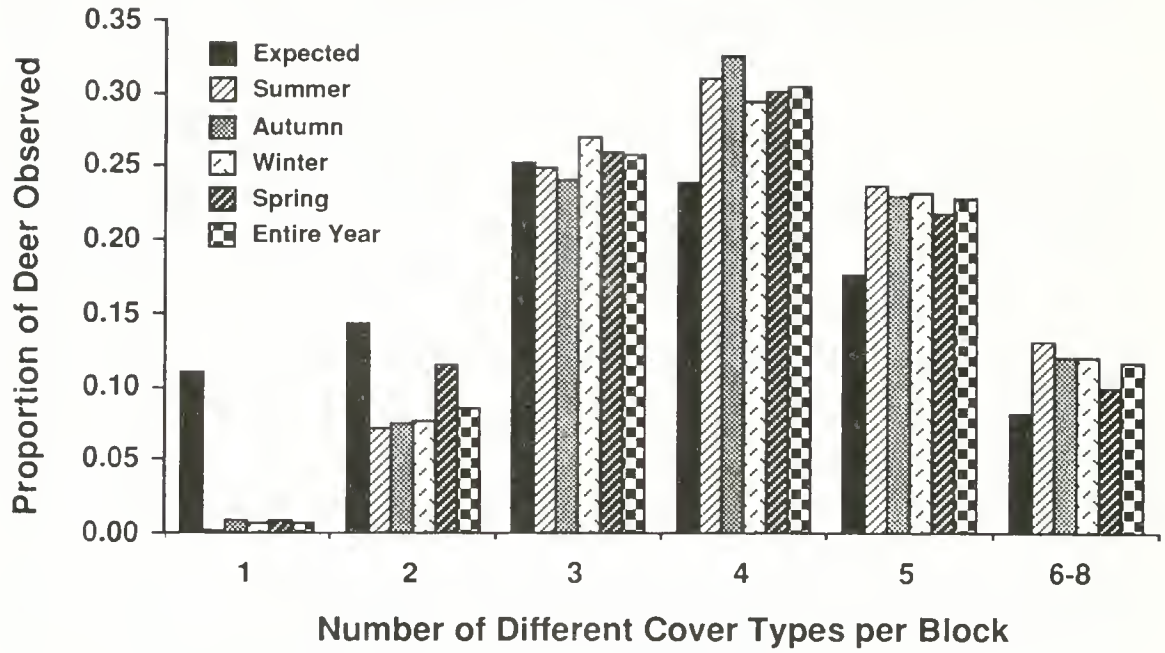


Figure 9.3. Annual and seasonal distribution of mule deer in relation to number of different cover types per 28.8 ha block.

expected, and blocks with 4 or more different cover types received greater than expected use. Once 4 cover types were included, the relative degree of selection increased only slightly to the maximum of 8 types found in any block. Deer use of the least diverse blocks (1 or 2 cover types) was highest in spring, coinciding with increased use of sagebrush-grassland vegetation.

Similarly, deer were not distributed randomly in proportion to the number of cover polygons available per block during any season (summer: $X^2 = 659.0$, 7 df, $P < 0.00001$; autumn: $X^2 = 583.6$, 7 df, $P < 0.00001$; winter: $X^2 = 1269.0$, 7 df, $P < 0.00001$; spring: $X^2 = 783.3$, 7 df, $P < 0.00001$). Fewer deer than expected occurred in blocks containing 1 to 3 cover polygons (Fig. 9.4), blocks containing 4 polygons were used as expected, and those containing 5-12 polygons were used by more than expected numbers of deer.

Influence of Topographic Diversity on Habitat Use

Deer did not use the 4 TOPOINDEX categories in equal proportion to availability during any season (summer: $X^2 = 654.3$, 2 df, $P < 0.005$; autumn: $X^2 = 709.5$, 2 df, $P < 0.005$; winter: $X^2 = 1316.7$, 2 df, $P < 0.005$; spring: $X^2 = 465.0$, 2 df,

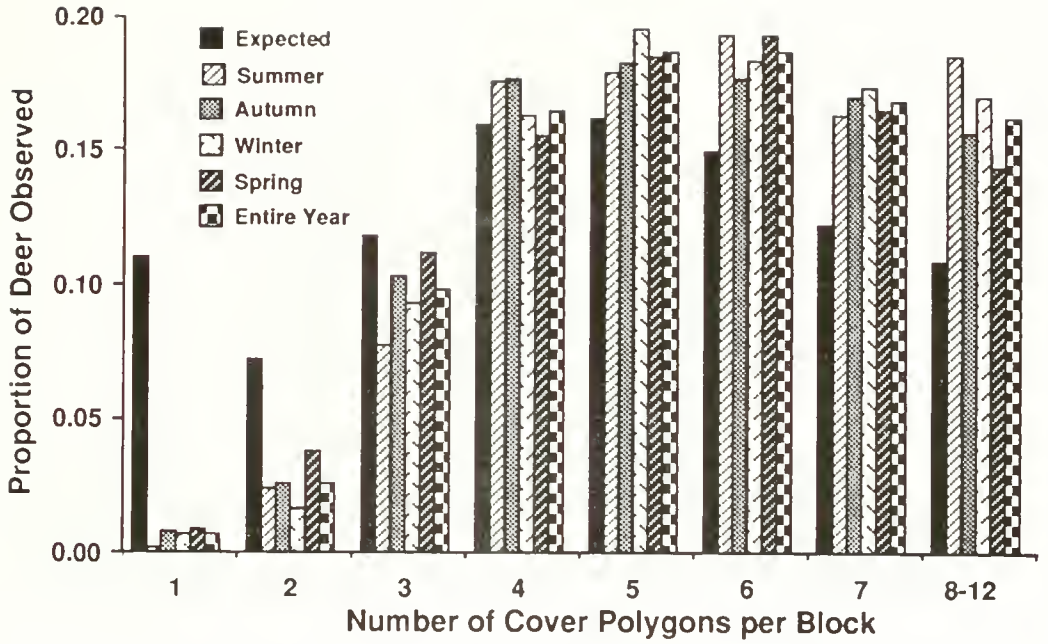


Figure 9.4. Annual and seasonal distribution of mule deer in relation to the number of different cover polygons per 28.8 ha block.

$P < 0.005$). Blocks of low relief were used much less than expected, while those of high relief, especially in the range of 150-230 m/km, were used much more than expected (Fig. 9.5). In spring, deer used blocks with low relief significantly more ($P < 0.001$) than during all other seasons, coinciding with use of sagebrush-grasslands on level to gently rolling sites. Average or above-average numbers of deer usually were observed during summer, autumn, and winter where relief values were 135 m/km or higher, and in spring where values exceeded 80 m/km.

Influence of Free Water on Habitat Use

Earlier, Mackie (1970) reported that 50.2% of the deer observed on the area during summer and 56.0% of those recorded in autumn were found within 0.805 km of a known source of free water, while 83.7% and 86.8%, respectively, occurred within 1.61 km of a water source. Those data have been misinterpreted to indicate that mule deer require free water and have been used to justify construction of additional reservoirs for livestock while citing wildlife benefits. This occurred even though Mackie (1970) noted (1) that the distances deer were observed from water generally reflected the distribution of water sources as well as deer, (2) few portions of the area were more than 1 mile (1.61 km) from water, and (3) distribution of water was not a significant factor influencing deer distribution even during most arid seasons or years.

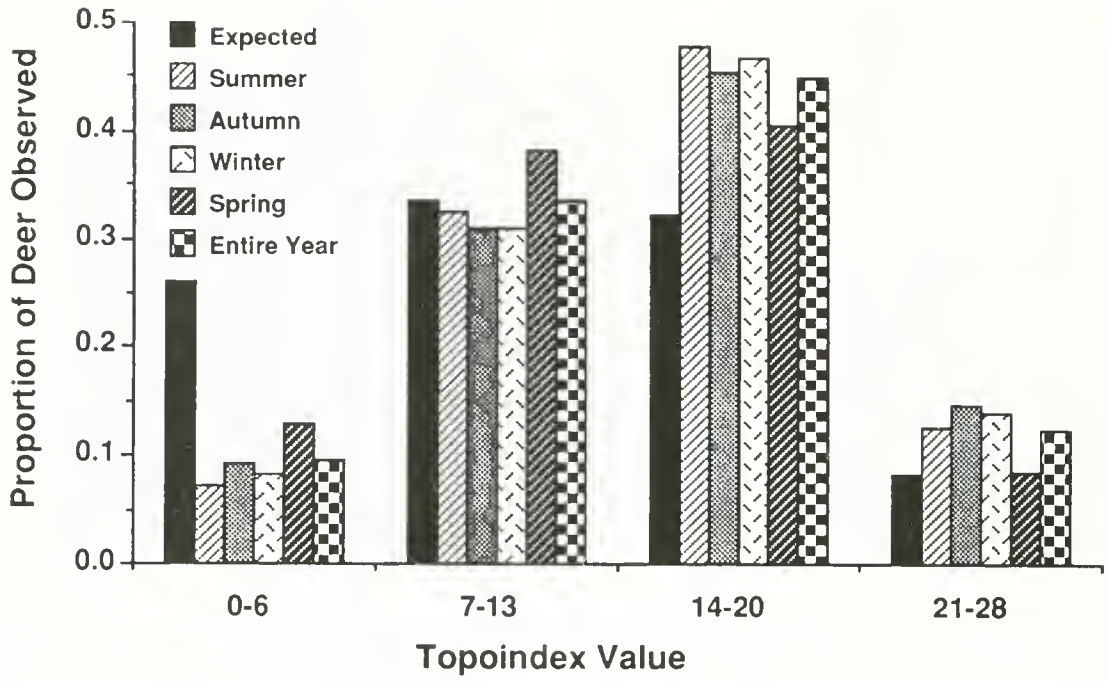


Figure 9.5. Annual and seasonal distribution of mule deer in relation to the degree of topographic relief. Increasing topoindex = increasing topographic relief (see text).

We re-examined the possible influence of free water on distribution and habitat use of mule deer on the area through the block analysis of data for 1976-1984. There were 63 known water sources on the area during that period as compared to 56 during 1960-1964. Of the 63, 44% were located in open sagebrush-grassland or broad coulee bottom habitat, 38% were on the edge of sagebrush and timbered vegetation types, and only 18% were within timbered types. Because of this, the visibility bias described earlier against observations of deer in timbered types from vehicle routes would also be expected to indicate greater than actual proportions of deer use close to water sources.

Analysis of deer dispersion during the wet summers of 1978 and 1979 showed that 43.9% occurred within 0.805 km of a water source and 89.9% were within 1.61 km. During autumn, those percentages were 41.4% and 88.4%, respectively. During the dry summers of 1980 and 1983, only 20.0% of the deer observed were within 0.805 km of a known water source, while 66.1% were within 1.61 km. During the subsequent autumn, those percentages increased to 30.6% and 73.9%, respectively.

Although the percentage of deer observed within 0.805 km of water in the current analysis was lower than reported for 1960-1963, this was expected based on changes in visibility bias between the 2 periods. The percentages of deer observed within 1.61 km of water was nearly the same throughout.

The high percentage of deer observed within 0.805 and 1.61 km of water during most seasons and years was not different from a random distribution. Very little of the study area was more than 1.61 km from water. During wet years, when all sources held water, 44.9 % of the 953 28.8-ha blocks were within 0.805 km of water and 89.0% were within 1.61 km. In addition, ephemeral water sources occurred throughout the area. During dry years, 31.9% and 74.4% of the blocks were within 0.805 km and 1.61 km, respectively, of a known water source and ephemeral water rarely occurred. The observed distribution of deer relative to distance from water was not different from that expected based on a random distribution during wet summers ($X^2 = 0.76$, 1 df, $P = 0.40$), wet autumns ($X^2 = 2.30$, 1 df, $P = 0.14$), or dry autumns ($X^2 = 0.94$, 1 df, $P = 0.36$). During dry summers, however, the observed distribution of distances at which deer were observed from water was significantly non-random ($X^2 = 107.6$, 1 df, $P < 0.001$). Examination of cell contribution to the total chi-square value indicated that significantly fewer deer than expected were observed in blocks within 0.805 km from a water source and significantly more than expected occurred in blocks more than 1.61 km distant from water.

Overall, proportions of deer observed at various distances from water were significantly different between wet and dry years both in summer ($X^2 = 141.2$, 3 df, $P < 0.005$) and autumn ($X^2 = 64.3$, 3 df, $P < 0.005$). Deer were distributed further from water during dry years than wet years. This indicated that deer did not move toward remaining water sources as reservoirs dried up as also was the case with deer distribution between the very dry year of 1961 as compared with 1960 (Mackie 1970).

This does not mean that free water was not important to mule deer. Rather, deer apparently can easily move 2.41 km or more to obtain free water if needed and water was sufficiently abundant and distributed to meet all seasonal and annual needs even during driest periods. During such periods, several marked deer were seen drinking from reservoirs up to 3.2 km from their normal home range. When disturbed they immediately returned to that home range. Thus, though deer may occasionally move long distance to water during dry periods, such movements are specific to that purpose and do not signify a general shift in home range closer to water sources.

Even if deer preferred to range close to sources of free water, several other factors may have led to their distribution at random or greater distances than expected from water. As stated earlier, 44% of all water sources on the study area were located within broad open sagebrush-grassland and coulee bottom areas. The lack of vegetational and topographic diversity may have precluded deer from spending more than minimal amounts of time in the vicinity of water in those habitats. However, deer spent considerable time in the open sagebrush-grassland type during spring when new, succulent green growth occurred in abundance. They also made increased use of the type following green-up in autumn and in foraging on rubber rabbitbrush during autumn and winter. This suggested that a lack of preferred forage also may have limited use of larger blocks of sagebrush-grassland, especially during hot, dry summers when they were distributed at greater than random distances from water. At that time, they probably preferred to remain near steep, timbered, north-facing slopes that retained at least some succulent forage. There were few water sources and thus reduced use by cattle near those sites, which left the succulent forage remaining in those areas primarily available to deer.

Livestock grazing patterns probably were also an important factor influencing deer distribution in relation to water. The broad open areas of sagebrush-grassland and coulee bottoms in which nearly half of all water sources were located comprised primary range for cattle (Mackie 1970). During most periods, but especially during hot dry summers, cattle were closely associated with water such that all areas, including timbered sites, within 0.805 km and up to 1.61 km or more from a water source were heavily used for feeding and resting. Although deer may have avoided such areas in part for social reasons, little quality deer forage remained available by mid summer. In the absence of cattle, deer may have made greater use of those areas and have been distributed closer to water, at least during hot, dry summers and autumns.

Patterns of Habitat Selection by Sex and Age Class

Vegetation Cover Types

Seasonal use of vegetation cover types was not statistically different among adult females, fawns, yearling males, and mature males (summer: $X^2 = 51.7$, 60 df, $P = 0.76$; autumn: $X^2 = 47.7$, 60 df, $P = 0.88$; winter: $X^2 = 39.7$, 60 df, $P = 0.98$). Possible differences could have been obscured by that test because non-productive females were often associated with males, and all females and fawns were often associated with yearling males during autumn and winter. To determine whether differences occurred between productive females and mature males, we further compared use of vegetation types by

fawns and mature males. Fawns and mature males used vegetation types differently during summer (X^2 = 16.8, 4 df, P < 0.005). Some difference may also have occurred during autumn (X^2 = 8.9, 4 df, P = 0.07), but there was no difference in winter (X^2 = 3.6, 4 df, P > 0.50).

Both fawns (and by inference productive females) and mature males used blocks containing Douglas fir-juniper types in greater proportion than availability, but selection for those types was strongest by fawns (Table 9.5).

Table 9.5. Observed proportional use of blocks containing various vegetation types by fawns and mature males compared with expected proportional use.

		Douglas fir-Juniper	Pine-Juniper-Shale	Pine-Juniper-Grass	Sagebrush Grassland	All Others
Summer	Fawns	0.207	0.183	0.218	0.258	0.134
	Mature Male	0.159	0.255	0.150	0.286	0.152
	Expected	0.132	0.147	0.186	0.377	0.158
Autumn	Fawns	0.210	0.172	0.218	0.240	0.160
	Mature Male	0.196	0.223	0.176	0.280	0.125
	Expected	0.132	0.147	0.186	0.377	0.158
Winter	Fawn	0.217	0.202	0.224	0.223	0.134
	Mature Male	0.187	0.214	0.201	0.238	0.161
	Expected	0.132	0.147	0.186	0.377	0.158

Similarly, both selected blocks containing pine-juniper-shale types, but here the strongest selection was by mature males. The pine-juniper-grass type was selected by fawns/productive females, but avoided by mature males. The differences were greatest during summer, when fawns were youngest and females with fawns generally isolated themselves from other deer, and declined through autumn and winter.

Possible differences in use of vegetation cover types between females and males were also tested by comparing vegetation composition of blocks most strongly selected by adult females with that of blocks most strongly selected by males through summer and autumn. Female-selected blocks were those in which the number of females observed was at least 3 times that expected with a regular distribution and no males were ever observed or, if males were observed, the ratio of females to males was at least 5 times greater than expected on

the basis of proportional distribution. Male-selected blocks were based on the same criteria, except that males predominated. Fifty two blocks were designated as female selected and 61 were male selected (Fig. 9.6).

The vegetational composition of female- and male-selected blocks differed significantly (X^2 = 378.1, 19 df, P < 0.001). Further examination indicated that the greatest difference was in occurrence of the pinus-juniperus-shale type, which was used more than expected by males and less than expected by females. The open and moderate density Douglas fir-juniper, scattered density pine-juniper-grass, moderate density pine-juniper, and river riparian cover types, in decreasing order of importance, were all used more than expected by females and less than expected by males. Non-timbered types, including shale-longleaf sage, sagebrush-grassland, and greasewood were more abundant in male-selected blocks, although individual contributions to the total chi-square value were not high.

These differences in selection of vegetation cover types between productive females/fawns and adult males were expected on the basis of cover and forage availability. Douglas fir-juniper and scattered density pine-juniper-grass types, selected by productive females/fawns, provided the greatest seasonal quantity and diversity of forage for deer (Tables 3.2 and 3.3). The pine-juniper-shale type produced the lowest quality and diversity of forage of any timbered type on the area and had greatest representation in blocks used predominantly by males. The Douglas fir-juniper and moderately dense pine-juniper cover types, most strongly selected by females, also provided the greatest amount of hiding cover among all major types.

Vegetational Diversity and Topography

Fawns and productive females used blocks containing more cover types than those used by mature males during summer (X^2 = 10.64, 5 df, P = 0.06), but not during autumn (X^2 = 7.62, 5 df, P = 0.19). Mature males were more likely to occur in blocks containing only 1 or 2 cover types than were fawns and productive females. Fawns and productive females also selected more diverse blocks than mature males based on number of cover polygons per block during summer (X^2 = 24.07, 7 df, P < 0.005), but not during autumn (X^2 = 9.05, 7 df, P = 0.25).

There were significant differences in distribution of fawns, females, and males among topographic relief classes during summer (X^2 = 21.2, 6 df, P = 0.002) and autumn (X^2 = 13.4, 6 df, P = 0.04), but not during winter (X^2 = 1.7, 6 df, P = 0.94). Fawns and productive females avoided areas of both extremely low and extremely steep terrain. Proportionately

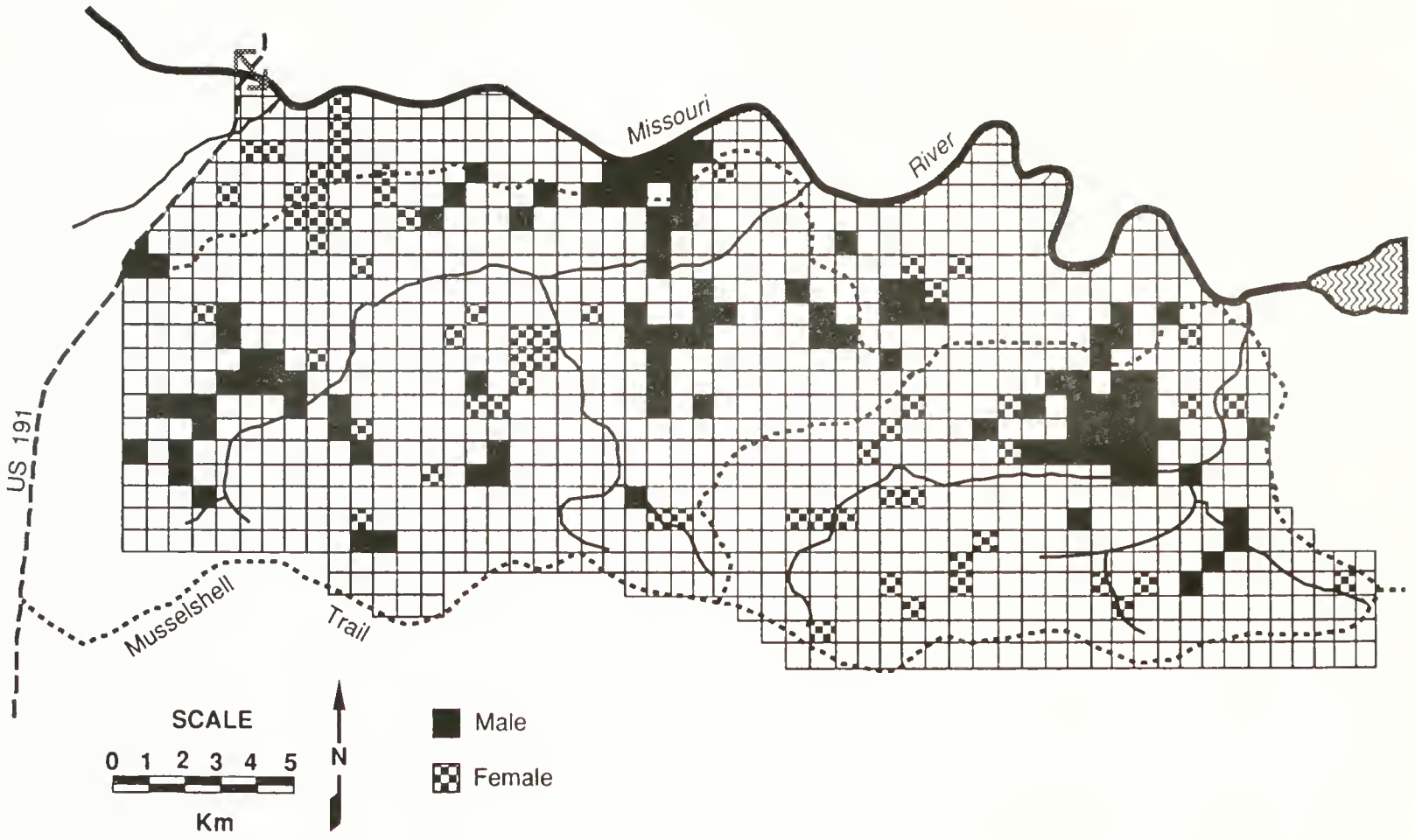


Figure 9.6. Distribution of blocks most strongly selected by males and by females. See text for selection criteria.

more fawns and productive females occurred in blocks of moderate to moderately-steep relief. Conversely, areas of low relief received disproportionately heavy use by males. Productive females and their fawns may have avoided extremely steep terrain because summer-autumn forage and hiding cover were lacking. Most of those areas had very sparse understory vegetation, were dominated by bare shale soil, and thus were poor fawn-rearing habitat.

Distance to Free Water

Because of the demands of lactation on adult females, we believed that fawns and productive females might be more closely associated with water sources than other deer, especially mature males, and that differences would be most evident during the driest summer and autumn periods. There were significant differences in distribution between fawns and mature males during dry summers (X^2 = 20.3, 3 df, $P < 0.005$) and dry autumns (X^2 = 15.93, 3 df, $P < 0.005$). However, while proportionately more fawns and productive females than mature males were observed within 0.805 km of water source, proportionately more fawns than adult males were also found in blocks more than 2.41 km away. This indicated that the distributional differences probably were not related to a requirement for lactating females and fawns to range closer to water than adult males. Other factors influencing distribution and habitat use apparently were overriding.

Relationship Between Mule Deer Density and Habitat Selection

Because mule deer were generally dispersed over more of the study area during periods of high as compared with low populations, it was possible that deer increasingly used less favorable sites with regard to vegetation cover types, habitat diversity, and topography as deer density increased. To test that hypothesis, we compared deer use of and selection for vegetation types, number of different cover types and cover polygons, and TOPOINDEX categories during summer-autumn between 1976-1978 and 1981-1983. Deer densities were lowest in 1976 and generally low through 1978; they were high during 1981-1983, with the peak in 1983.

There were no differences in deer distribution by cover type between the 2 periods (X^2 = 23.4, 20 df, $P = 0.27$). Thus, it appeared that most of the increase in deer numbers occurred in blocks that were vegetationally similar to the "core" blocks used during the population low, and little increased use of less preferred habitat occurred. It is possible that much preferred habitat became vacant during the population decline of 1972-1976, and subsequent increases were restricted largely to those areas.

There were significant differences in the distribution of deer relative to the number of different cover types (X^2 = 16.9, 5 df, P = 0.005) and the number of cover polygons (X^2 = 33.6, 7 df, P < 0.001) per block between the periods of low and high density. Although deer, generally used the lowest diversity classes more during the period of high density, much of the chi-square value was contributed by seemingly random, non-logical variation among higher diversity classes. To determine if there was significantly less use of low diversity blocks at low densities, the diversity classes were combined into 2 categories; one included the 3 lowest classes, the other all other classes. The difference in distribution with respect to diversity was still significant for both number of cover types (X^2 = 3.46, 1 df, P = 0.07) and number of cover polygons (X^2 = 6.06, 1 df, P = 0.02) per block. Much lower than expected use of low diversity areas by deer at low densities (1976-1978) made the major contribution to the total chi-square values. Based on the distribution of mapping units, it appeared that most of the difference occurred because of greater selection against large areas of sagebrush-grassland dominated habitat away from and on the fringes of timbered areas during the period of low deer numbers. This difference was not apparent in the test for difference in the kinds of cover types in blocks because deer had continued to use blocks that included smaller patches of Sagebrush-Grassland through the population low.

No significant differences were detected in deer distribution in relation to topographic relief classes between high and low population densities (X^2 = 1.14, 3 df, P = 0.77).

Seasonal Differences in Habitat Use Among Migratory Deer

Migratory deer monitored during 1976-1984 generally moved to one of 7 "wintering areas" within the study area. Because most deer were "residents" and did not move long distances between summer and winter ranges, we believed that comparison of habitat characteristics of summer and winter ranges of migratory deer would help explain winter habitat requirements of mule deer with respect to environmental conditions that prevailed during the study.

There were significant differences in the vegetation cover types characterizing summer and winter areas (X^2 = 3204.7, 19 df, P < 0.0005). Types prevalent on winter ranges included: burned, open, and scattered density classes of Douglas fir-juniper; open and scattered density pine-juniper-shale; shale-longleaf sage; silver sagebrush; and river riparian types (Table 9.6). Those prevalent on summer ranges were open and moderately dense pine-juniper-grass, sagebrush-grassland, and grassy bottom types. Winter areas also were characterized by greater numbers of cover types and cover

Table 9.6. Habitat variables with significantly greater representation in either winter or summer use areas of migratory mule deer.

Variable	Winter Areas	Summer Areas	Significance level
Vegetation Cover Types		open Douglas fir-Juniper	Z=6.1,P<0.0000
	scattered Douglas fir-Juniper		Z=7.3,P<0.0000
	burned Douglas fir-Juniper		Z=8.0,P<0.0000
	open Pine-Juniper-Shale		Z=5.2,P<0.0000
	scattered Pine-Juniper-Shale		Z=4.0,P<0.0001
	Shale-Longleaf Sage		Z=7.9,P<0.0000
	Greasewood		Z=6.7,P<0.0000
	Silver Sagebrush		Z=4.0,P<0.0001
	River Riparian		Z=3.6,P=0.0003
		moderate Pine-Juniper-Grass	Z=2.7,P=0.006
		open Pine-Juniper-Grass	Z=2.5,P=0.01
		Sagebrush grassland	Z=-11.3,P<0.0000
		Grassy Bottoms	Z=-2.2,P=0.03
Number of cover types per block	+		Z=5.6,P<0.0000
Number of cover polygons per block	+		Z=5.5,P<0.0000
TOPOINDEX value	+		Z=10.4,P<0.0000

polygons per block and steeper terrain than summer range areas.

Migratory deer generally moved from areas of low relief at the heads of drainages along the southern edge of the area to areas of steep terrain near the Missouri River. Thus, most of the difference in habitat characteristics between seasonal ranges was apparent without statistical tests. The interpretive problem related more to separation of cause and effect and elimination of possible spurious relationships.

Steeper terrain containing adjacent north- and south-facing slopes appeared to be the most important factor distinguishing winter from summer ranges of migratory deer. Differences in vegetation cover types and diversity followed differences in terrain and thus did not appear to be the primary determining factors in deer preference for those areas. For example, the 2 eastern wintering areas lacked the Douglas fir type, 5 of the 7 lacked the silver sagebrush type, and 3 lacked the river riparian type. On the other hand, steep terrain generally held lesser snow depths and provided thermal environments more favorable to deer survival than level or rolling terrain. North-facing slopes usually were dominated by timbered types with dense overhead cover that further reduced snow depth and provided thermal cover. South-facing slopes generally were more open, providing for rapid snow melt as well as warm areas for resting and foraging on sunny days.

Mule Deer Habitat Use in Relation to Elk and Cattle

A prior publication (Mackie 1970) focused specifically on habitat use relationships between mule deer, elk, and cattle on the study area during 1960-1964. Although we do not propose to review those relationships in detail, data obtained from subsequent studies, especially during 1976-1984, enabled us to re-examine previous conclusions based on additional information and different analytical techniques.

Data on numbers and general distribution of elk were recorded during all aerial surveys in winter 1964-1975. During 1976-1984, numbers and locations of all elk observed during seasonal aerial surveys were recorded identically to those for mule deer and were compiled and analyzed using block analysis. Time and other considerations precluded us from collecting quantitative data on cattle distribution or habitat use after 1963. Thus, conclusions relating to mule deer-cattle relationships can only be reviewed qualitatively on the basis of general observations and additional studies conducted on the supplementary NCRCA during 1972-1975 (Knowles 1975, Komberec 1976, Campbell and Knowles 1978) and during our studies in 1976-1986.

The range use and food habits data obtained during 1960-1964 indicated that opportunities existed for competition between mule deer and elk and between mule deer and cattle on the study area. The probable degree of competition was light, except for some seasons. The greatest overlap in range use and food habits of deer and elk occurred during the period from April to September, while that between mule deer and cattle occurred in April and May. Opportunities for competition in spring centered around intensive use of the sagebrush-grassland type by all 3 species. The potential for competition between mule deer and elk during summer was related to significant use of timbered vegetation types and similar forage plants by both species. In addition, competition could become more severe; 1) during periods of drought, 2) if stock water sources were constructed on terminal portions of large ridges or on smaller ridges within timbered breaks and extended intensive grazing to those areas, or 3) if numbers of elk using the area increased greatly.

Considering relative distribution and varying intensity of use of the area by mule deer, elk, and cattle on a yearlong basis, there was little overlap between primary cattle range areas and primary mule deer habitats (Fig. 9.7). Primary areas for use by cattle were the broad open plains, major open ridgetops, and larger coulee bottoms. Mule deer primarily used steeper, diverse or timbered terrain between major ridgetops and major coulee bottoms. Comparison of overall spatial distribution of mule deer and elk also indicated relatively little overlap, especially when seasonal patterns were considered.

Mule Deer and Elk

A comparison of the yearlong density distribution (intensity of use) pattern for elk during 1976-1984 (Fig. 9.8) with that for mule deer (Fig. 7.1) indicated little overlap in areas of greatest intensity of use for both species. A simultaneous plot of the 2 highest categories of intensity of use for both species (Fig. 9.9) indicated only 11.2% of the high density blocks for both species were the same. Of high density elk blocks, 26.9% were also high density mule deer blocks and 19.1% of high density mule deer blocks were also high density elk blocks.

The general pattern of dispersion of elk on the study area, however, was similar to that for mule deer. That is, moderate to dense concentrations generally extended across broken terrain along slopes and coulees between major ridgetops and major coulee or river bottoms. Thus, the primary habitat for elk and mule deer centered in and around essentially the same land areas, although areas used intensively by elk extended on to primary cattle range more so

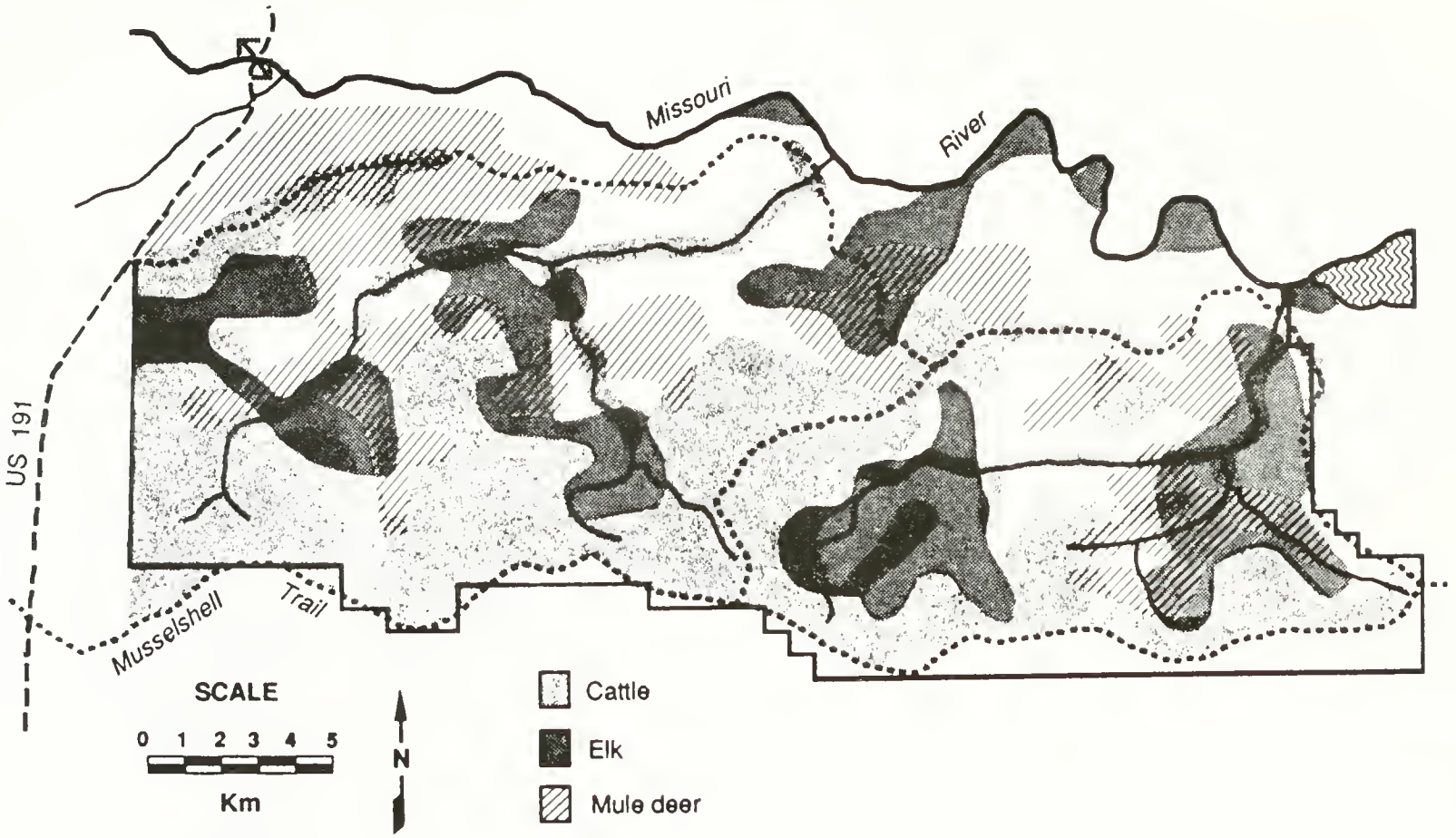


Figure 9.7. General distribution pattern of mule deer, elk, and cattle indicating the areas most intensively used by each species.

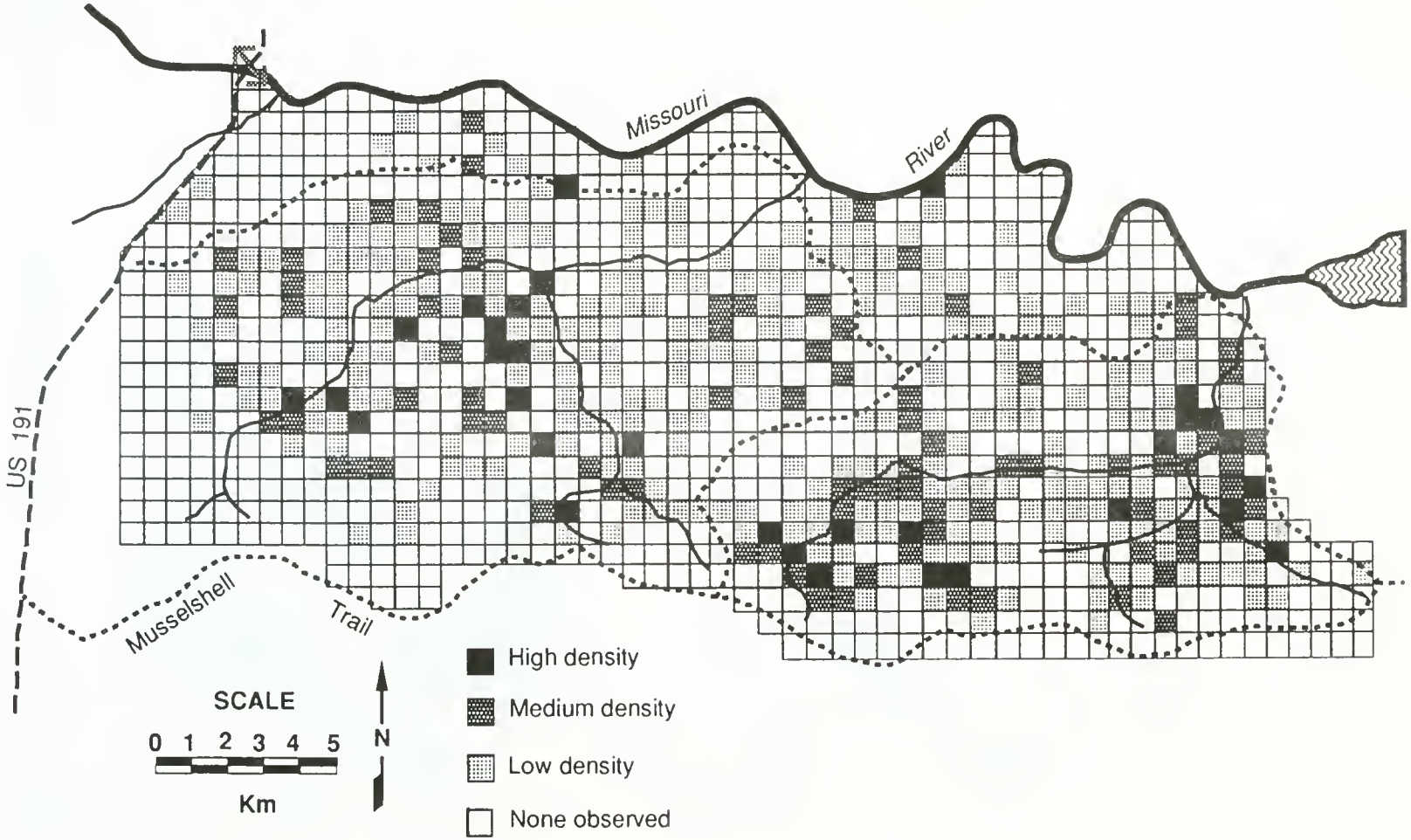


Figure 9.8. Relative density distribution (intensity of use) for elk as determined by data from 32 aerial surveys during 1976-1984.

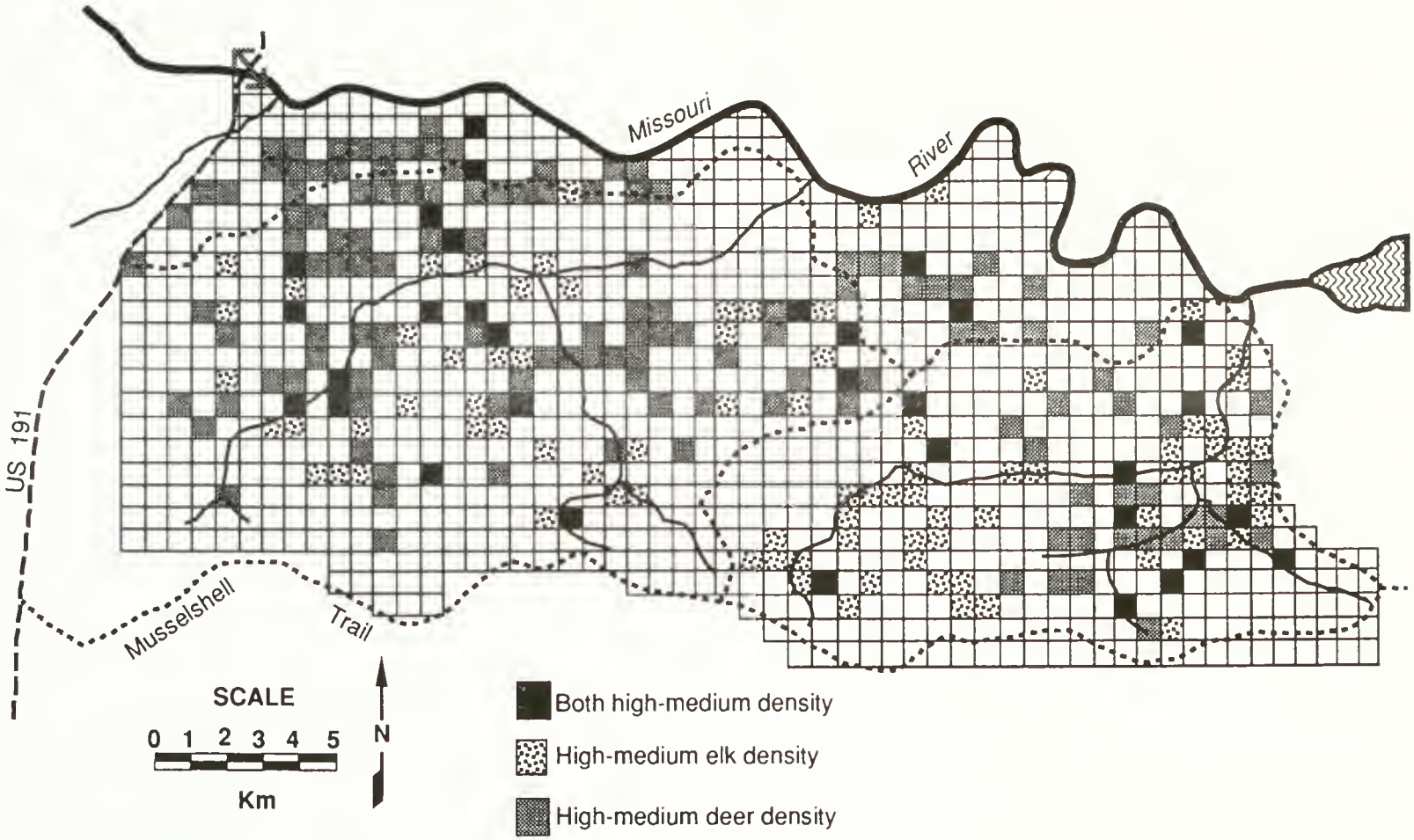


Figure 9.9. A plot of areas of high and moderate intensity of use for mule deer and elk, indicating degree of overlap.

than mule deer. Within the broad distribution, elk use was also centered around areas of high density ("core areas") surrounded somewhat concentrically by areas of lower elk use. This dispersion pattern was much less distinct than for mule deer. This may reflect the fact that elk are highly gregarious, occurring in relatively large groups, and move widely within relatively large home ranges. The fact that there was relatively little sympatry in high density areas between mule deer and elk indicates that, as elk numbers have increased, differences in habitat requirements or preferences have enabled both species to use the area such that they exist with minimal conflict.

Among vegetation cover types making up major portions of the area, elk showed distinct preference on a yearlong basis for the moderately dense Douglas fir-juniper type, the open and scattered density pine-juniper-shale types, the moderately dense pine-juniper-grass type, and the grassy coulee bottom type. The first 3 were also preferred by mule deer.

Elk use of vegetation cover types was different among seasons (X^2=631.7, 60 df, P<0.0001). Major contributions to total chi-square value were made by selection for the river riparian type during autumn, greasewood and silver sagebrush during winter; and an overall lesser degree of use of timbered types and increased use of the sagebrush-grassland type during spring.

Use of vegetation cover types by mule deer and elk differed during all seasons (summer: X^2=145.7, 20 df, P<0.0001; autumn: X^2=129.4, 20 df, P<0.0001; winter: X^2=260.7, 20 df, P<0.0001; and spring X^2=214.3, 20 df, P<0.0001). During summer, elk used the moderately dense pine-juniper-grass type more than mule deer, while mule deer used the scattered and burned Douglas fir-juniper and shale-longleaf sage types more than elk. During autumn, elk made significantly more use of the river riparian and moderately dense pine-juniper-grass types than mule deer. Mule deer made more use than elk of the scattered and open density Douglas fir-juniper types and shale-longleaf sage type during autumn. Elk used the greasewood and silver sagebrush types more than deer during winter, when mule deer used all Douglas fir-juniper types and the scattered density pine-juniper-grass type more than elk. During spring, mule deer used the burned Douglas fir-juniper and open pine-juniper-shale types more than elk. Elk made greater use of pine-fir-juniper, moderately dense pine-juniper-grass, pine-juniper-shale, and grassy bottom types than mule deer.

Yearlong, elk used the most dense conifer cover types and the dense river riparian type more than mule deer (X^2=87.2., 1 df, P<0.005). There was also a significant difference in

the seasonal use of dense cover types by elk (X^2=51.9, 3 df, P<0.005). The greatest use of dense cover occurred during autumn in association with the hunting season. The lowest use of dense overhead cover types by elk was during winter when use of dense overhead cover was highest by mule deer. Campbell and Knowles (1978) reported similar findings from their study of elk in the "River breaks" habitats north and east of our study area.

Habitats used by mule deer and elk also differed significantly in the number of cover types occurring per block during all seasons (Chi-Square tests, all P's <0.0001). During summer and autumn, mule deer used more diverse areas (more cover types/block) than elk. During winter, however, elk used areas with more cover types/block than mule deer. Although number of cover types in blocks used by mule deer and elk were significantly different during spring, interpretation of the results was difficult. Elk used areas with 1 and 3 cover types/block more than mule deer, while mule deer used areas with 2 cover types/block more than elk. Use of areas with 4-8 cover types/block was similar between mule deer and elk. These results observed for blocks with 1-3 cover types may have occurred because, during spring, elk ranged further into the open sagebrush-grassland type. When not in the open, they were well within the timbered types. Mule deer, on the other hand, generally used the sagebrush-grassland type in close proximity to timbered cover. This "edge effect" resulted in mule deer distribution in blocks containing 2 cover types while elk were more likely to be either in the open (1 cover type) or well within timbered habitat (3 or more types).

Differences in the number of cover polygons among blocks (Chi-square tests, all P's <0.0001) were similar to differences in numbers of cover types/block. The only major difference between the 2 parameters occurred during winter when mule deer used the most diverse and the least diverse areas more than elk, and elk used the middle spectrum of diversity more than did deer. During all seasons, mule deer used areas with greater topographic relief than elk (Chi-square tests, all Ps <0.0001).

During dry autumns, mule deer and elk were not distributed differently in relation to distance to water sources (X^2=6.22, 3 df, P=0.10). During all other seasons in both wet and dry years, mule deer and elk were distributed differently (Chi-square tests, all P's <0.005) in relation to distance to water sources. During both wet and dry summers, a significantly greater proportion of elk than mule deer were within 0.805 km of water. During wet summers, more elk were also observed at 1.61 km or more from water. A greater proportion of mule deer than elk was from 0.805-1.61 km from

water during wet summers and from 0.805-2.41 km during dry summers. During wet autumns, more elk than deer were distributed within 0.805 km and at greater than 2.41 km from water. During winter and spring, when the availability of free water might be considered least important, deer were significantly closer to water sources than were elk.

Mule Deer and Cattle

Although some changes in livestock grazing patterns on the study area occurred and may have influenced changes in spatial distribution between periods of intensive study in the early 1960s and 1975-1986, the lack of data on cattle distribution and habitat use precluded statistical comparisons with distribution and habitat use by mule deer and elk. Our observations generally supported those of Mackie (1970). During hot, dry summers and autumns, cattle made much more extensive use of timbered areas and second and third order drainages than during wet or "normal" years. This indicated they could potentially have an impact on deer at that critical time. However, because most heavy use of timbered types by cattle was near water sources during hot, dry periods and much of the timbered types did not contain water sources, potential impacts were somewhat reduced.

As discussed in Chapter 7, we believe it possible that some changes in distribution of mule deer between the 1960s and the 1970s and 1980s may have been related to changes in the distribution and seasonal grazing patterns of cattle. Because of the lack of quantifiable data, however, we cannot prove that those changes were more than coincidental.

Campbell and Knowles (1978) indicated that highly mobile elk actively selected rested pastures over grazed pastures in a rest-rotation system in the Missouri River Breaks (NCRCA) and selected the most lightly grazed areas in other grazing systems. The shifting of elk distribution away from areas of intensive use by cattle could result in increased competition between elk and less mobile mule deer.

All of these considerations indicate the potential for impacts on mule deer by cattle grazing, but we have no evidence that mule deer populations were adversely impacted. One problem with investigating impacts of cattle grazing on wildlife in the western United States is that there are few or no areas of significant size where livestock grazing in some form does not occur. Thus, we know nothing about mule deer distribution, habitat use, and population performance in the absence of livestock. The mule deer distribution, food habits, habitat use, and population performance we report probably all reflect adaptation to the long-term presence of cattle.

Effect of Cattle and Elk on Mule Deer Population Performance

Most studies on the effects of livestock grazing on deer have documented differences or overlaps in food habits, distribution, and habitat use. Few, if any, have documented population impacts. We have data on mule deer population performance under a season-long grazing system over a long period of time, and also have data to compare between season-long and rest-rotation livestock grazing systems. We could not detect any differences in mule deer fawn survival or population trend for the 2 grazing systems.

Mule deer population trend was the same for both grazing systems during 1975-76 through 1986-87 (Figure 9.10). Any differences that may have occurred were too subtle to detect from our population estimates. The 2 pastures of the rest-rotation system that were within "breaks" mule deer habitat encompassed 202 km^2 compared to 275 km^2 for the season-long grazing system. Mule deer density during spring ranged from 0.5 mule deer/km^2 to 3.4/km^2 on the rest-rotation system and from 1.4/km^2 to 4.5/km^2 on the season-long grazing system. We believe those differences were related to habitat structure and composition rather than grazing systems.

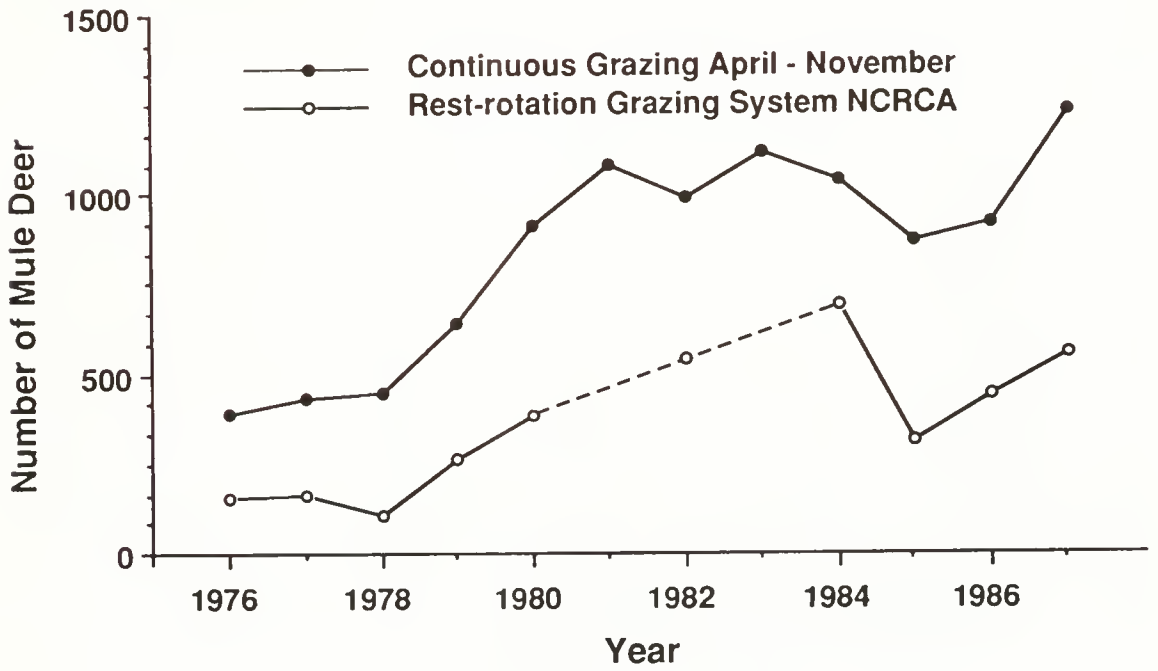


Figure 9.10. Spring mule deer population trend within a season-long and a rest-rotation grazing system, 1976-1987.

The available data did not indicate any consistent pattern of better fawn survival for one grazing system over the other or one grazing treatment over the others within the rest-rotation system (Table 9.7). The data indicated higher fawn survival during spring 1984 and 1985 within the rest-rotation system. However, those data were collected 1-2 months earlier than on the season-long grazing system and mortality continued through the period, at least within the continuous grazing system. Subsequent population estimates (Figure 9.10) indicated that fawn survival probably also declined within the rest-rotation system after the aerial survey, especially during 1985. Annual changes in fawn survival appeared to be more similar than different between the 2 grazing systems and appeared related more to common environmental influences than to differences in grazing systems.

Table 9.7. Fawn:100 adult ratio during spring for mule deer inhabiting a rest-rotation grazing system and a season-long grazing system in the Missouri River Breaks, Montana.

Year	NCRCA (Rest-rotation) Pasture 3	NCRCA (Rest-rotation) Pasture 4	NCRCA (Rest-rotation) Combined	South-side Study Area Season-long Grazing[a]
Spring				
1976	2[Hb]	10[R]	6	11
1977	24[V]	38[H]	28	30
1978	9[S]	18[V]	12	26
1979	40[R]	41[S]	40	65
1980	81[H]	66[R]	77	82
1981	--	--	--	61
1982	--	--	--	44
1983	--	--	--	59
1984	32[H]	30[R]	32	13
1985	36[V]	45[H]	39	5
1986	26[S]	21[V]	24	18
1987	68[R]	63[S]	66	65

[a] Season-long grazing, April 15 - November 15.

[b] H = Heavy use April - August.
R = Pasture rested entire year.
V = Pasture used June - November.
S = Pasture used August - November.

If further study of the effects of livestock grazing on deer in this environment is desirable, it might require that 1 large study area (150-250 km^2) be established with no livestock grazing in order to compare mule deer habits and population trend in the absence of livestock grazing with data from grazed systems.

Because cattle may displace elk to some extent (Campbell and Knowles 1978) and diets of mule deer and elk overlap more closely than diets of mule deer and cattle (Mackie 1970), elk may potentially compete with mule deer. However, increasing numbers of elk in recent years did not keep the mule deer population from increasing as well (Fig. 9.11). During 1960-63, Mackie (1970) estimated by unduplicated counts from the ground and air that a maximum of about 100 elk used the area. Aerial counts during winter from 1963 to 1975 ranged from 5 to 136 elk, indicating little change in the elk population from around 100 elk during the period 1960-1975. Numbers remained relatively stable through 1979, after which the number of elk on the study area increased steadily until an average of 306 elk used the area for the combined autumn, winter and spring seasons by 1986 (Fig. 9.11). Average numbers for the 3 seasons were used to represent elk populations because many of the highly mobile elk do not remain within our study area yearlong. In recent years, the number of elk using the area has increased from autumn through spring. During 1986-87, 169 elk were counted during autumn, 334 during winter, and 415 during spring. During 1976-83, when counts were also made during summer, elk numbers on the area were generally higher during summer than in any season except spring.

The mule deer population reached 2 succeeding all time peaks despite a 3-fold increase in elk numbers over 20 years. More elk were on the area during spring 1987 than mule deer during the low in spring 1976. To this point, increasing numbers of elk have not resulted in declining mule deer populations. We do not know, however, if the mule deer population increase would have been greater if no elk were present or if an increase in elk numbers beyond current levels will affect mule deer populations. Given the reduced hunting pressure on female mule deer and the broad environmental fluctuations since the mid-1970s, we can determine no significant impact on mule deer populations attributable unequivocally to competition with cattle or elk. Certainly, major changes and trends in mule deer numbers during 1960-1987 did not appear significantly affected by competition with cattle or elk.

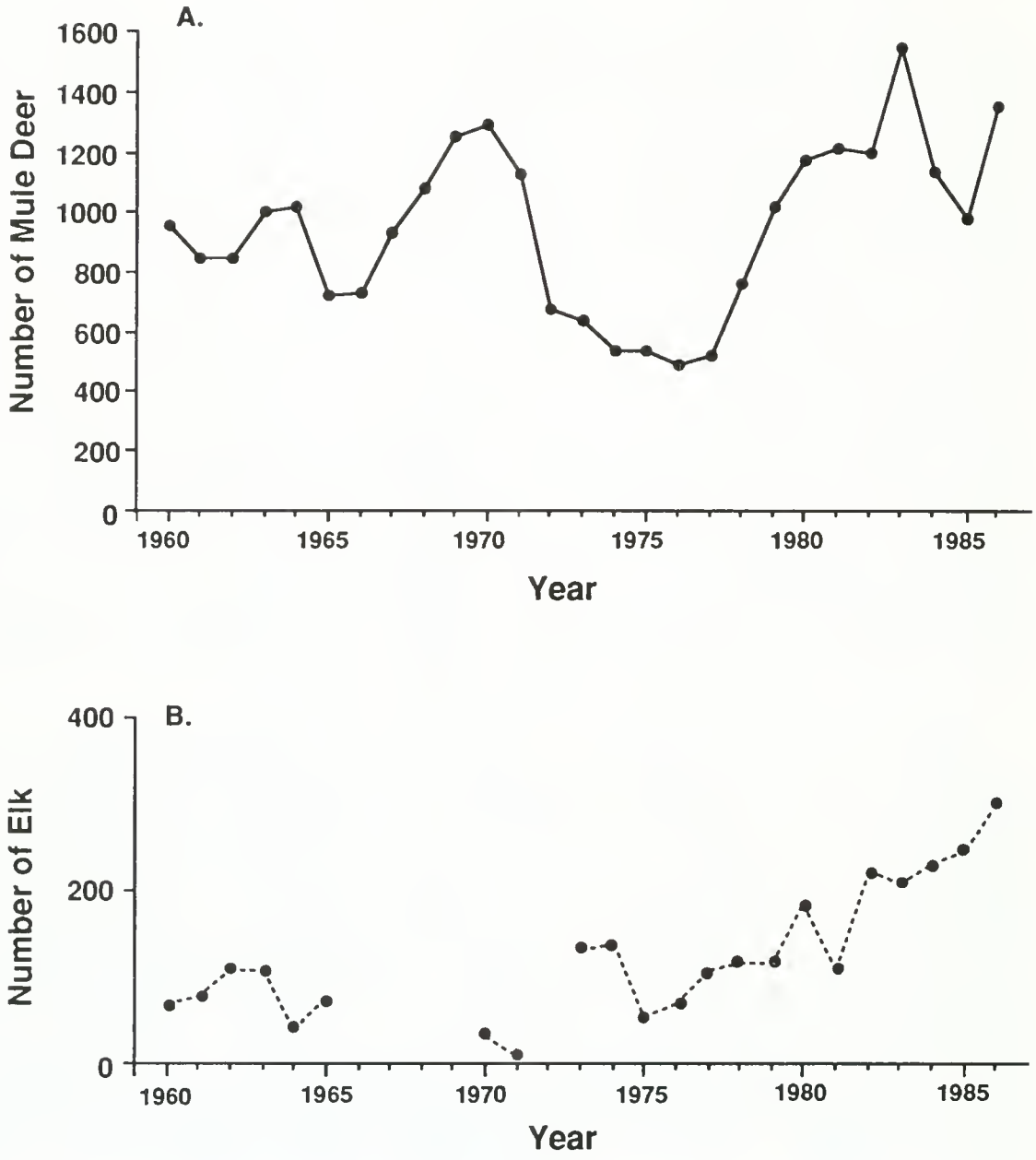


Figure 9.11. Population trend of mule deer (A.) and elk (B.) on the study area, 1960-1986.

Summary and Discussion

Mule deer made use of most of the area in some way at some time during the study. Habitat diversity, by itself, appeared to be a good predictor of long-term intensity of use by mule deer. Over time, intensity of use was highest for areas with the most topographic and vegetational diversity. Vegetational diversity often followed from topographic diversity; thus, topographic diversity may be the major or ultimate factor influencing mule deer use of an area.

The Douglas fir-juniper vegetation cover types were most preferred. These types provided hiding cover and succulent forage during summer and autumn and thermal cover during winter. They received minimal use during spring when deer preferred more phenologically advanced non-timbered types for feeding. The Douglas fir types generally occurred on steep north-facing slopes and were usually bordered by pine-juniper-shale and shale-longleaf sage types on the adjacent south-facing slopes. Although lacking in forage, these south-facing slopes provided lesser snow depths and warm resting areas during sunny winter days. No types provided yearlong habitat by themselves, so diversity within small areas was important in determining quality mule deer habitat.

Habitat use by productive females and their fawns differed from that of mature males during summer and autumn. Females and their fawns made more intensive use of areas and vegetation cover types that provided the best forage and cover. Similar findings were reported by King and Smith (1980), Bowyer (1984), and Ordway and Kransman (1986). The reduced competition between males and their offspring was predictable based on kin selection and breeding strategy.

Although the relative use of preferred vegetation cover types did not change between low and high deer densities, deer made increased use of areas with lower overall diversity at high densities. This indicated that although sagebrush-grassland was still not a preferred type at high deer densities, deer made increased use of areas near large patches of sagebrush-grassland at population highs. At low deer densities, most use of sagebrush-grasslands was of small patches interspersed among other types. Also, little difference in use of vegetation cover types was apparent between low and high densities because even at high densities, the majority of the deer were still in areas dominated by preferred vegetation cover types.

Distribution of water sources apparently was not extremely important in determining mule deer distribution and habitat selection. At the least, the current distribution of water is adequate for the needs of deer. Further water

development would increase cattle use of areas now preferred by deer and could result in increased impact of cattle on deer.

We can only speculate about habitat preferences and use of mule deer, elk, and cattle in the absence of each other. All data were collected during periods when all 3 species were present and thus reflect mutual adaptation to the presence and activities of the others. Considering seasonal use patterns, there appears to be little conflict between mule deer, elk, and cattle at current population levels. Although habitat use by mule deer and elk overlaps more than that of mule deer and cattle or elk and cattle on an annual basis, potential conflict was reduced because of seasonal differences in the use of preferred areas. It is possible that any one species, in the absence of the others, might use the environment more loosely (in a coarse-grained manner). As a result of long-term coexistence, all 3 species may have evolved a more "fine-grained" pattern of use that reduces direct competition.

Campbell and Knowles (1978) reported that home ranges for elk on this area varied from 75 to 448 km^2 or 2 to 13 times the size of the largest mule deer home ranges. That mobility enabled elk to take advantage of seasonal and temporarily available preferred habitats throughout a wide area rather than remain within a small area and compete for seasonally dwindling resources. Over time, elk have evolved a strategy that most efficiently utilizes resources over a broad area, thereby reducing potential conflicts in any one area. However, because of similarities in food habits between elk and cattle and the desire for an economic return from their investment, ranchers may perceive conflicts between elk and cattle at current population levels.

There was generally little overlap in distribution, habitat use, or food habits between mule deer and cattle. The greatest potential competition between cattle and mule deer probably occurs during droughts when cattle make more use of areas preferred by deer. During those periods, however, there would be very little quality forage available for deer even if no cattle were present. It is likely that grazing by cattle reduces forage for deer on the edges of current mule deer habitat (e.g. the heads of drainages and boundaries of sagebrush-grassland and grassy bottoms with forested types). These areas appear to be marginal deer habitat, and even in the absence of cattle, might receive significant use by deer only at high population densities. Thus, the absence of cattle on the area might result in somewhat higher deer populations at peak densities when marginal habitats are filled. However, deer in these areas are those most vulnerable to severe winters with deep snow and to severe drought, therefore any increase in deer numbers that might

result from the absence of cattle would be extremely ephemeral.

The long-term impacts of cattle grazing on mule deer may include some beneficial effects. For example, local "overgrazing" by cattle, although undesirable from the standpoint of range management, may have resulted in increased vegetational diversity and abundance of forbs and rubber rabbitbrush on small ridges and along edges of timbered and sagebrush-grassland types.

CHAPTER 10

POPULATION-HABITAT RELATIONSHIPS

Habitat relationships refer to the manner in which animals in a population interact and respond behaviorally and biologically to characteristics of and changes in the habitats/environments they occupy. These relationships, along with direct human exploitation, constitute the 2 most important factors involving wildlife management (Peek 1986). They involve and integrate all aspects of habitat usage that influence the occurrence, numbers, and dynamics of animals in populations over time. Because of this, they inevitably also involve questions such as "what is carrying capacity" and "what ultimately regulates a population."

For the last 50 years, management of most North American ungulates has proceeded on the assumption that the amount of forage available is the major factor influencing carrying capacity and ungulate population size and dynamics. The accompanying assumption has been that the number of ungulates (density) is the major factor influencing forage quantity. The herbivore-vegetation interaction determines carrying capacity and population dynamics. From this also developed both the premise that deer and other ungulates if left alone will overuse their forage resources thereby lowering the "carrying capacity" (Caughley 1979), and the corollary that they must be cropped below "K" (ecological carrying capacity) to insure less time-lag fluctuations in the population and to provide larger, healthier, more productive animals. These assumptions resulted in the "principles" of compensatory mortality and reproduction.

A more developed discussion of the concept of carrying capacity, its origins, and usages was presented previously in the Introduction (Chapter 1). Data from our study area and population indicated that relationships between habitat-forage factors and deer population ecology and dynamics were much more complex than we originally believed based on the concepts and "principles" of deer biology applied in management at the time the study began.

Mule Deer-Forage Interactions

Forage Quantity

Our data documented extensive variation in the quantities of forage produced and available to mule deer on the study area. Over an 11-year period, 1976-1986, the quantity of forbs produced varied by about 16-fold and that of grasses by about 4.5-fold from the lowest year of production to the highest. The production of 3 shrub species varied by more

than 5-fold over a shorter 7-year period that did not include the year of lowest forb production. Additionally, an index of tree growth (Tree Ring Laboratory, University of Arizona, Tucson, C. Stockton and D. Meko, personal communication), indicated that over the 21-year (1960-1980) period, which encompassed most of the study, annual growth of Douglas Fir trees varied 10-fold from the poorest (1961) to best (1978) year. For a 100 year period (1881-1980), annual growth varied 21-fold from poorest (1956) to best (1916) years.

Most of the variation was inherent in the environment, controlled by climatic/weather factors (temperature and precipitation), and independent of influences of deer use or density. The maximum observed difference in deer numbers for the same season (3-fold) or among seasons over all years (4.4-fold) was considerably less than the variation in forage conditions.

The data also indicated that, during most years, fawn production and survival to December was directly related to an index of forage production; population change was directly related to fawn production and survival. There were several reasons why population numbers did not vary as widely as forage production. Biologically, fawn production and survival is limited and cannot exceed certain levels in any year regardless of how good forage conditions may be. Similarly, fawn survival can only decline to zero, no matter how poor the conditions, though adult mortality may increase. Also, relieved of lactation, adults can survive on poorer quality forage than lactating females require. Time-lag responses to wide fluctuations in forage production could occur as exceptionally good conditions result in fat accumulation, and exceptionally poor conditions result in fat depletion.

Further examination of our data, however, led to the conclusion that it was unlikely that fawn survival and population performance was directly related to forage quantity, or that deer numbers (density) influenced subsequent forage production. Very conservative estimates of annual forage production during the period 1976-1986 indicated that annual forage quantities were adequate to support 2-10 times the numbers of deer that occurred on the area during summer and autumn. A possible exception occurred during 1985, though given the conservative estimates and an "autumn green-up" it is also unlikely that the quantity of forage was deficient during 1985. Furthermore, the leaves and buds of fragrant sumac, snowberry, rose, and choke- cherry were never observed to be close to completely utilized. Those forages, which were important summer forages for deer, were nutritionally adequate to supply at least maintenance requirements (8-13% protein, Eustace 1971, Pac 1976, Mackie et al. 1979) for adults during most years.

Still other evidence that the quantity of forage, by itself, was not influencing deer population dynamics was provided by examination of interactions between fawn survival, antler size (condition) of yearling males, and numbers/density of deer on the area. Although fawn survival and antler size of yearling males were correlated to estimates of forage production, neither was correlated with the number of deer eating that forage. If deer and their forage supply interacted in a density-dependent manner we should have observed a significant interaction between fawn survival and antler size of yearling males with estimates of forage quantity and deer numbers. Addition of deer numbers to multiple regressions did not add significantly to the observed relationship.

There also was no evidence that browsing by deer subsequently reduced important browse plant populations or browse forage production. Deer utilization of rubber rabbitbrush, an important autumn-winter forage species, remained near 100% annually throughout the study, regardless of deer population level. Despite this and 2 deer population "peaks and crashes", rabbitbrush plant populations at least remained stable, and may have increased on the study area. Some plant species, perhaps because of their biology and season of use, tolerate browsing far above levels previously considered to be "over browsing" while maintaining productivity (Pellew 1984).

Similarly, the number and size of fragrant sumac plants was at least stable to increasing on most transects despite heavy use by deer during some years and severe girdling by microtine rodents during other years. The degree of use of current annual growth for fragrant sumac was not directly related to deer numbers. Relatively light use occurred at both low and high deer populations. Relatively heavy use was often but not always associated with drought conditions. The number of snowberry and rose plants declined as forest succession closed the canopy, but these plants increased in some areas following fires. The major shrub species used by deer during winter, big sagebrush and Rocky Mountain juniper, were essentially unlimited in abundance and did not show "classical" signs of heavy use such as "highlining" or "clubbing".

Overall, trends in forage plant abundance and production did not appear influenced measurably by deer browsing. Any annual or long-term changes that occurred were influenced more by climatic factors and/or successional changes related to forest maturation and periodic wildfires.

We also found no relationship between "key" browse plant abundance, production, utilization, and condition trends and

deer population trends and dynamics. Deer numbers fluctuated widely through the years, and in recent years were as high or higher than at any time in the past, while browse plant abundance was relatively unchanged. During periods when there appeared to be some general correlation between deer numbers and utilization, use tended to follow rather than precede changes in population size.

Deer population trends and dynamics through and following severe winters were particularly enlightening with respect to the role and importance of winter range and forage supplies. During several of the most severe winters (e.g., 1968-69, 1977-78, and 1978-79) when deer were most concentrated and forage and winter range were most limited, mortality of both fawns and adults was light to moderate. Subsequent fawn production and survival was generally high. In fact, fawn production and survival in 1979, following what may have been the most severe winter during the study, was the highest recorded. Those trends clearly were influenced by range forage conditions the previous summer and other interacting factors, not by the amount of winter range or "key" browse forage available. Such findings lead us to question the generalization or "principle" that winter range and forage supplies are invariably limiting, or that winter, when range and forage is most limited, represents the "bottleneck" in deer management in northern environments.

Because these findings contrast sharply with long-prevailing concepts, perhaps it is necessary to ask why and what, if anything about the study, study area, or findings differed significantly from other works.

Most studies related to deer have been short term and concerned primarily with either plants or animals. Few, if any, studies have been long term and coupled information simultaneously on ungulate and plant demography (Macnab 1985). Thus, our information on the relationship of forage quantity and deer numbers may not really be an exception when compared to the few other studies that collected information on both plant and animal numbers. We can compare our findings with at least 2 other studies on mountain-foothill ranges where mule deer were dispersed during summer but typically very concentrated during winter. One major interpretive difference is that our data were collected for a deer population that remains relatively dispersed over its range except in the most severe winters.

Studies by Wallmo et al. (1977) of a migratory mule deer population in north central Colorado indicated that forage quantity on summer through early winter range was enough to support more than 30 times the number of deer that actually occurred. Forage quantity on late winter range would have

supported 1.25-2 times the number of deer that occurred. The quantity of forage was adequate at all times, but the nutritional quality of winter forage would not sustain deer at any population level. The duration and severity of winter was the factor determining the length of time that deer could survive on these ranges (Wallmo et al. 1977).

Studies in the Bridger Mountains of Montana (Mackie et al. 1976, Hamlin 1977) indicated that what had been considered the 2 "key" browse species on winter range supplied sufficient forage to support less than one-third of the mule deer that occurred. The remainder was provided by plants that had previously been considered of poor quality or unimportant. This situation had existed for years because plant density and forage production had apparently not changed from prior years when up to twice as many deer occurred on the winter range. Total forage quantity was adequate, but nutritional level of the winter diet was at maintenance levels or below (Morton 1976).

Harvesting to reduce the degree of use by deer on "key" browse species in the Bridger Mountains would have required reducing the deer population from about 200 deer to somewhere below 60 deer. Similarly, utilization of rubber rabbitbrush, a "key" forage plant in the Missouri River Breaks, was never below 69 % and usually above 80% even at very low deer population levels. As referred to earlier, trying to balance winter deer populations with "key" species considered to supply adequate quality forage will lead to the "ridiculous conclusion that the only good herbivore population is one vanishingly small" (Sinclair 1981).

Where data are available for deer populations in northern environments, summer forage has generally been shown to be available in more than adequate quantities. In most cases, as indicated by the studies cited above, the quantity of winter forage also appears to be adequate, but its nutritional quality is inadequate to support any deer for long periods. The accumulation of fat reserves during summer and autumn, winter growth dormancy by the animals, and behavior oriented toward energy conservation are all strategies adopted by northern cervids for the normal situation of nutritionally inadequate winter forage (Klein 1985). Production and survival of deer in these environments thus appears to be influenced primarily by the length of time that deer can use good to adequate quality forage, allowing them to accumulate fat reserves. This is balanced by the length of the winter period (or period of using low quality dormant forage), and the severity of the winter period as it determines energy demand.

Forage Quality

As discussed earlier, annual variations in the length of time plants remain green and succulent, providing high quality forage, appeared to be a major factor influencing mule deer population dynamics on our study area. Both our observations and those of Blaisdell (1958) indicated that high forage production was correlated with delayed maturation, hence the apparent relationship between population dynamics and forage quantity. However, delayed maturation as a result of cool spring temperatures also provided a longer period during summer and autumn that high quality forage was available, providing adequate forage for lactation through summer and fat accumulation prior to winter. Late summer and early autumn rains that resulted in an autumn green-up of grasses during 1962, 1977, 1985, and 1986 provided a longer period of high quality forage and resulted in high fawn production and survival during 1963, 1978, 1986, and 1987. High total precipitation for the 10 months prior to the growing season also influenced fawn production and survival as long as above average growing season temperatures did not result in early plant maturation.

We agree with Klein (1985) that maximization of selective feeding by cervids is most likely to occur in mountainous regions where wide variability in exposure, slope, and altitude create a diversity of microclimatic influences. The distribution, habitat use, and home range patterns of deer on our study area indicated similar conclusions. Deer, especially females with fawns, preferred the most topographically and vegetationally diverse areas and were able to utilize smaller home ranges in those areas.

In contrast to mountainous areas, however, the elevational gradient on our study area was relatively small. In northern mountainous areas, green forage is always available until autumn frosts, even during dry years. On our study area, forage maturation and desiccation was delayed somewhat on steep north- and east-facing slopes during average to good years, but during extremely dry years, most forage became desiccated on even those sites by early August. For example, the leaves of deciduous shrubs remained green during most years until the first frost or early September, but deciduous shrubs dried out and the leaves turned colors and dropped by late July in 1961 and 1984, even on north-facing slopes. After that time, even non-productive adult deer were probably on no better than maintenance diets for the remainder of the year.

All of our data indicated that the length of time that high quality, green, succulent forage was available had a major impact on fawn survival and thereby population dynamics.

That relationship occurred independently of deer density. It may still be argued that we overlook the importance of forage quantity because during some years deer face a shortage in the quantity of quality forage. We do not deny that argument has merit; the point remains however, that we found no evidence that quantity or quality of forage available was adversely impacted by deer, either by measurement of the vegetation or by detecting density-dependent relationships for fawn production and mortality.

Generally, the growing season on our study area was short, with most herbaceous plants maturing by late July in most years. Because there was little elevational gradient on the area, forage desiccated rapidly on all areas when severe drought occurred; plants on north- and east-facing slopes remained green only a few weeks longer than those on other sites. Also, north- and east-facing slopes (the Douglas fir and Pine-Juniper-Fir types) comprised only 15.7% of the study area. Thus, even if plants/forage on those areas remained green much longer than plants on other areas, only a portion of all deer, which remained widely dispersed on the study area, could take advantage of them. Certainly, deer that occupied home ranges including those types faced better living conditions during all years, but parturition territoriality functioned to limit the number of deer that live in such habitats during summer and early autumn when availability of green, high quality forage was critical.

Conditions that led to a reduction in the quantity of quality forage were not related to deer numbers or to "overbrowsing" or "overgrazing" by deer; thus, a reduction of the number of deer in areas where forage was of poor quality would not increase the survival of other deer in that area. Forage quantity and quality on this area were determined primarily by annual variations in precipitation and temperature. How individual deer fared under the varying annual conditions depended, at least in part, upon where they lived, the topography, vegetation, weather/climate, and other land use within that area.

Contributions of the Fixed-Stable Habitat Base to Population Dynamics.

The deer-forage relationships just discussed are only one aspect of population-habitat relationships. Much of the important deer-forage relationship was part of the dynamic-variable habitat component of our model (Fig.1.4). However, fixed-stable properties of the habitat model such as topography and habitat structure interacting with the variable habitat components and the morphology, physiology, and behavior of the deer (animal component, Fig.1.4) also played a major role in population ecology and dynamics.

Even within one study area or one broad ecological zone, topography, vegetation and habitat types, microclimates, other land uses, and the presence and activities of other animals may vary widely. Either a verbal or quantified description of an area varies depending on the resolution used in examination and description. Grossly, all parts of our study area were more similar to each other than to western mountainous areas or more eastern plains. However, at medium to fine resolution, no 2 parts of the area were exactly alike. All deer home ranges within the study area differed structurally, in the kind, amount and quality of resources available, in the juxtaposition of resources, and in the manner in which individual deer exploited the area and its resources. Thus, the habitat was heterogeneous and deer behavior, performance, and fates were heterogeneous (an individual deer was not equal to 1/N).

Mule deer distribution, movements, food habits, and habitat use were determined by the interaction of social organization and other aspects of behavior with topography, climate, vegetation production, and land use. That interaction and annual variations in weather, vegetation production, and human and coyote predation influenced the occurrence and densities of deer as well as patterns of reproduction and mortality. Examination of interactions helped explain not only annual variations in deer density within place, but why "average" density varies from place-to-place.

Our data indicated that mule deer preferred relatively steep terrain to areas of low relief. Some habitat types, such as the Douglas-fir juniper types, were preferred over others and some types were used more during one time of the year than during others. Overall, mule deer preferred areas that were the most topographically and vegetationally diverse. Movement strategies and home range size and pattern of use varied by sex, reproductive status, area occupied, and annual and seasonal variation in weather. Distribution of deer density (dispersion) varied across the area, with total deer numbers, by sex, and by reproductive status. Data on mule deer distribution, home ranges, and habitat use, along with data on reproduction and mortality, indicated that not all parts of the area were equal in their ability to provide for the long-term needs of deer. Some areas provided relative stability in deer density and performance, while others varied considerably from year to year in their ability to support deer as weather and other factors varied. Annual changes in density, reproduction, and mortality recorded for the population as a whole were made up of a composite of histories and fates of individual deer (Fig.1.4), each of which faced somewhat different circumstances.

The density of deer in a given area increased only within certain limits, probably as influenced by the interaction of parturition territoriality and other aspects of social organization with the fixed habitat base. Most of the increase in deer density on the study area from 1976 to 1983 was the result of deer occupying previously unused areas rather than substantial increases within areas of preferred habitat.

The structure of the habitat in an area, as influenced by topography and vegetation, probably influences maximum deer density. Habitat structure and diversity also influenced the available resources, including the quantity and phenology of forage (Klein 1985) and the occurrence and adequacy of sites to ameliorate harsh winter conditions. Hiding cover, availability of alternate prey, and predator effectiveness can also be influenced by topography and habitat structure. For example, those deer that had home ranges bordering on the river and reservoir were more vulnerable to coyote predation during winter because of the ice, despite relatively good forage conditions in those areas.

Habitat structure probably also influences the number of parturition territories that an area will support. The more topographically and vegetationally diverse areas not only supplied a more varied and long-lasting source of quality forage, but more rugged terrain also provided a greater degree of visual isolation of deer from each other. Thick timber can produce visual isolation and succulent forage during late summer and autumn, but forage quantity is generally reduced in thick timber and that type does not provide quality forage during spring because of delayed phenological development. Relatively open areas, however, that contain many different slopes and exposures as a result of closely interspersed ridges and valleys can provide as effective of visual isolation for parturient females as thickly timbered areas.

The degree of visual isolation an area provides may influence how many adult females an area can support before aggression by parturient females results in emigration by yearling females. Rugged, diverse "core areas" provide habitat that will support the most females and fawns over the greatest variety of environmental conditions. Beyond the limits that those areas provide for non-conflicting parturition territories, excess production must disperse to areas that are unoccupied during the fawn-rearing period. Such dispersal provides for maximal occupancy of the environment.

Based on comparison between our findings and data available from studies on other areas in Montana, we hypothesize that habitat structure also at least partially

influences adult sex ratios observed on an area. Sex ratios in mule deer populations across the broad spectrum of habitats occupied is not always correlated with obvious mortality factors such as hunting that impact males more than females. There are, for instance, mule deer populations that experience much lighter hunting pressure than deer on our study area but maintain much lower adult male:female ratios.

During summer and early autumn, distribution and habitat use of mature males was significantly different from that of females and fawns. Females and fawns occupied sites and habitats that were more diverse, with better forage and cover components than areas occupied by mature males. Significant differences in habitat use were not apparent during late autumn and early winter. It appeared that the aggressive behavior and dominance of parturient females during late spring and early summer determined home range location and distribution for all deer. Parturient females appropriated optimal fawn-rearing habitat and other deer, including non-productive females, yearling males, and mature males generally had fit in to any areas not occupied by productive females. Those areas may be adequate to support non-lactating adult deer, but will not, at least consistently, support lactating females. Yearling deer must establish in areas where there are no deer or where they are tolerated by existing deer. In some areas and some years, that can mean emigrating from the population.

For purposes of illustrating our hypothesis, we assume that 4 categories of habitat occur: 1) optimal fawn-rearing habitat, 2) sub-optimal habitat, allowing adult survival, but not fawn survival during some years, 3) marginal habitat, where adults may survive with specialized habitat use and movements, but few, if any, fawns are recruited, and 4) non- or only transiental deer habitat. Adult sex ratio may be at least partially determined by the relative proportions of these 4 types of habitat within the area surveyed. Relatively high proportions of sub-optimal and especially marginal habitats may be necessary for an area to support many adult males. There are some areas that contain habitat that support recruitment of fawns and everything else around it is non-deer habitat. Tentative indications are that these areas generally have low adult male:female ratios. The adult males could certainly live and survive in the fawn-rearing habitat, but few find places to live that are not occupied by agonistic females during the fawn-rearing period; thus most males must emigrate to other areas, out of the population.

Sub-optimal and marginal areas also provide less habitat that will support deer during the most extreme conditions such as drought and severe winters. As the population increases during years or periods of years of good conditions for fawn

production and recruitment, dispersal of females and yearling males resulting from parturition territoriality fills in more and more sub-optimal habitat. When environmental conditions reverse (drought and severe winters), those dispersers that established a migratory tradition are able to maintain relatively better living conditions by migrating back to core areas during autumn and winter, after productive females become more tolerant of other deer. Females living in marginal habitat that did not establish a migratory tradition are subject to poorer forage quantity and quality during late summer and autumn as well as deeper snow and colder effective temperatures during winter. Those females and their fawns are more vulnerable to mortality from all sources.

Because of this, fawn production and deer mortality are in a sense "density-dependent", although not in the classical manner. At higher densities, more deer live in "marginal" habitat and are subject to higher rates of mortality. Increased mortality results not because of a measurable reduction in the food supply owing to intra-specific competition, but because more deer are occupying habitats in which they are vulnerable to drought and severe winters. During the most extreme conditions, females in core habitats may not recruit fawns, but resources within their home range are adequate for survival of non-productive adults. During extreme environmental conditions, some marginal habitats may not provide even for the survival of adults. Dusek et al. (1989) expressed similar views regarding population regulation in white-tailed deer on the Lower Yellowstone River of Montana. They indicated that socially influenced resource partitioning relegated younger females to sub-optimal habitat, resulting in lower productivity. The importance of habitat patchiness and a combination of optimal and suboptimal habitat to population dynamics has also been noted for snowshoe hares (*Lepus americanus*) (Wolff 1980) and California voles (*Microtus californicus*) (Ostfeld and Klosterman 1986).

The weather and climate of an area has both stable, predictable characteristics and variable, unpredictable characteristics. Winter months are predictably colder than other months, vegetation is dormant, and snow cover is often present. Deer adapt to this predictability by undergoing winter torpor (Silver et al. 1969) and practicing energy conservation by establishing home ranges that include south- and north-facing slopes that provide reduced snow depth and relatively warm microsites during the day and at night, respectively. Vegetation-forage conditions are predictably the most favorable each year during late May and June, even during dry years. The predictability of the general weather pattern results in late November breeding and June parturition dates, when the combination of sufficient time for recovery from winter, succulent forage during lactation, and adequate time

for growth of fawns and recovery of females prior to winter are, on average, most advantageous (Klein 1985). Short-term variation in the weather is much more unpredictable. One winter may be much longer and more severe than another and one summer-autumn period may be much more arid than another. These short-term differences in weather can result in great annual differences in the rate of accumulation and use of fat reserves.

We believe that much of the difference in potential density of deer between areas is established by the stable, predictable properties of the environment such as topography, soil fertility, general climate-weather pattern, and major habitat types and their structure. Whether the deer population is at the potential level or somewhere below that density depends on annual variations in weather and other factors that influence the amount of effective habitat.

Discussion

It is apparent that there is an interaction between the habitat, its use by deer, and the population dynamics of the deer. Not all habitat is equal in providing for the needs of deer. During favorable periods, deer can successfully utilize sub-optimal and marginal habitats by adopting specialized habitat use and movements strategies, such as autumn-winter migration, that enable them to fill their needs. During extreme environmental conditions, even normally optimal habitat on this area may temporarily fall short of supplying the needs of deer. Deer utilizing sub-optimal habitat may not be able to successfully use compensating strategies at all during those periods. When environmental conditions deteriorate to such an extent that compensating strategies of habitat use are not adequate, fawn production and survival and even adult survival declines; first in marginal habitats and later in sub-optimal and optimal habitats if unfavorable conditions persist very long. The behavior of mule deer on this area, centering on parturition territoriality and a matrilineal social structure, along with the length of favorable environmental conditions establishes the relative proportions of deer inhabiting areas that are optimal or less than optimal for reproduction and survival.

An area in the same general location as our study area, that had less topographic relief, providing less vegetational and phenological diversity, and the drainages oriented in different directions (i.e., with more east- and west-facing slopes and fewer south- and north-facing slopes) would probably average a lower density of mule deer over time. There would be fewer permanent home range sites that would give deer visual isolation during fawn rearing and also allow them to compensate for severe winters or drought.

Both Mackie (1978) for mule deer and Dusek et al. (1988) for white-tailed deer have indicated that deer density increased as the diversity, complexity, and stability of the environment increased. Generally, the degree of topographic relief, by itself, indicates the degree of diversity on an area. Other aspects of diversity such as vegetation types, microsites, and phenological development, follow from topographic diversity. However, anything that increases diversity, such as small agricultural fields, patchy or variable grazing, or some fires, could also increase stability and average deer density.

Given the fixed-stable habitat constraints and the morphological, physiological, and behavioral constraints within which the population functions, "average" deer density across the entire area is determined by the length of time that dynamic-variable habitat conditions remain either favorable or unfavorable. During favorable periods, deer can survive and reproduce across most of the area. During unfavorable conditions, most deer may not successfully reproduce at all, and many adults living in marginal areas die. This view is similar to that of Thompson (1929) and Andrewartha and Birch (1954) in that the most important way in which animal populations are limited is "by the shortage of time when the rate of increase, r, is positive." That time is never very long on environmentally variable areas like our study area.

Thus, our view is that there is a "balance" in the dynamic-variable component of environment which interacts with the fixed-stable habitat base and the animal component. This interaction produces behavioral and biological responses in individual animals that result in individual consequences in recruitment and mortality. The sum of these individual consequences is "population dynamics" (Fig.1.4).

This view contrasts with the traditional, popular, and compelling ("it has to be true") concept of a "balance of nature". The "balance of nature" view implies density-dependent regulation involving a feedback loop between animals and their food supply (herbivores and plants, carnivores and prey).

The "balance in the environment" view is unpopular because it does not imply neat and tidy regulation. If the environment fluctuates too widely or changes its character, populations can become extinct, especially locally. We maintain that this is precisely what has happened and continues to happen. This is why viable populations exist in some places and not in others and why species population densities vary across their range. For the most part, however, the environment fluctuates ("balances") within

predictable bounds and populations adjust to this environmental fluctuation.

CHAPTER 11

POPULATION DYNAMICS

The population data obtained on our study area depict a mule deer population which, following recovery from near extirpation in the 1930s, has fluctuated widely for at least the past 30 years and presumably since the initial peak in numbers during the late 1940s (Fig. 4.7). Specific data for the past 28 years (Fig. 4.1) indicate declines spanning 2 to 5 years occurred during the mid 1960s, the early-mid 1970s, and the mid 1980s. Relative peaks occurred in the early 1960s, 1970-1971, 1983, and 1987. The major fluctuations involved 2- to 4.4-fold decreases or increases between low spring and high autumn numbers.

In addition to year-to-year and periodic fluctuations, large within-year changes in numbers of mule deer occurred during all years. Because of this, mule deer numbers were seldom stable from year to year during the same time period. Spring populations, measured after most annual mortality had occurred, were most stable but the "normal" range of fluctuation remained large.

All fluctuations were the result of changes in reproduction and mortality. For this discussion, immigration and emigration were included as special cases of reproduction and mortality, respectively, because consequences to population numbers were similar. Understanding the dynamics of regulation in Missouri River breaks mule deer thus requires that we address factors influencing variation in reproduction and mortality and how they interact to ultimately determine deer numbers over time.

Variation in Reproductive Rate

Although reproductive output varies to some extent in all populations, it has seldom been found to vary enough to indicate significant "self-control" by a population (Lack 1954, Caughley 1977). Mule deer on our study area were no exception. Fawn production varied from a high of 1.48 fawns per female to a low of 0.99 fawns per female within the extremes in environmental conditions and deer densities that prevailed during the study. Reproductive effort was at the low observed levels during and following drought, especially if deer had been very productive for several years prior to the drought.

Thus, in the most "restrained" situation, about 50 female fawns were added for every 100 adult ($\geq$ 1 year) females in the population during June, and about 50 male fawns were added for

every 50 adult males assuming an approximate 1 male:2 female adult sex ratio. Without additional mortality, the highest observed reproductive rate would result in a doubling of a population of 100 adult females and 50 adult males (an instantaneous growth rate of 0.69); at the lowest observed reproductive rate, population growth would be only slightly reduced to an instantaneous rate of 0.51. Because natural mortality was low, averaging only 7.2% in years when females were not hunted, the observed "reproductive restraint" (including both intrinsic and extrinsic factors) was not, by itself, sufficient to halt growth of the female population. As is the case for most populations, substantial mortality of fawns and greater than average mortality of adults must occur to achieve a stable population.

Other data on reproduction and age-specific mortality of adult females also indicated that little, if any, effective "reproductive restraint" was inherent in the population. Essentially all adult females initially produced fawns at the maximum rate their body condition allowed. A high rate of initial production apparently is less costly than rearing fawns (Short et al. 1969), and the initial effort can be terminated prior to or during early lactation if necessary. It also provided maximum opportunity for successful reproduction during years when quality of habitat resources for rearing fawns were good.

In highly variable and unpredictable environments such as our study area, the trait of initially producing maximum numbers of fawns during all years apparently maximizes the opportunity for females to pass on their genes. Recruitment of fawns in alternate years (Mundinger 1981) or producing fewer fawns during all years, are apparently not successful strategies in this environment because these females are no more successful than others in rearing fawns during years of poor conditions. Such strategies of reproductive restraint might be selected for in harsh, but stable and predictable environments where conditions for fawn rearing are seldom exceptionally good.

The environment of our study population is not only variable and unpredictable, but includes an effective natural predator. Living conditions for deer can swing rapidly from exceptionally good to exceptionally poor, and both favorable and unfavorable conditions often prevail over several consecutive years. In this situation, the best reproductive strategy appears to be to initially produce young at maximum rates each year to take advantage of favorable conditions for recruitment as they occur. Given the relatively short reproductive life of mule deer on the area, it seems most adaptive for a female to have the maximum potential to respond to good conditions, should they occur during her lifetime.

The longer the relative reproductive life span, the more likely "reproductive restraint" becomes adaptive.

Population theorists, beginning with Malthus and Darwin, traditionally have looked at the impressive reproductive potential of most populations and concentrated their efforts on the role and importance of mortality in population regulation. This view forms the basis for much current population theory. In harsh, variable, and unpredictable environments, however, it may be equally valid to assert that high reproductive potential is necessary to cope with inherent regular or periodically high mortality (Fisher 1930, White 1978). Although changes in reproductive rates, by themselves, were not sufficient to significantly regulate population growth of deer on our study area, reduced reproductive rates usually coincided with high fawn mortality after birth; they often coincided with increased adult mortality as well. If reduced reproductive rates and high post-partum mortality rates often resulted from the same ultimate factor(s), variations in the operation of such factor or factors may explain much of the variation in deer numbers.

Variation in Mortality Rate

The relative intensity of operation or relaxation of factors affecting mortality rates of fawns and adults appeared to exercise the greatest impact on population growth rates and trends. It should be noted, however, that from the standpoint of population dynamics and regulation, the role and impact of fawn mortality differed from that of adult mortality. Factors affecting fawn mortality determined annual recruitment to the adult segments of the population, whereas those affecting adult mortality determined losses. Also, the relative importance of various mortality factors differed between fawns and adults. This, plus the fact that our data indicated recruitment to the reproductive population was not effectively achieved until individuals were at least 1 year old, required that mortality rates and causes for fawns and adults be addressed separately.

Fawn Mortality

Annual mortality rate of fawns varied considerably among years (17-94%) and population trend generally followed the trend in fawn mortality by 1 year. Most mortality occurred during summer (ave. 65%), but seasonal rates varied widely among years.

Predation by coyotes was the single most important mortality factor for fawns, accounting for 88% of all deaths of radio collared fawns and 85% of deaths in summer and autumn. Overall, coyote predation on fawns was generally

lower during autumn than other times of the year. Only 9.1% of all deaths of marked fawns during 1976-1986 occurred during autumn. During the early-mid 1970s, 1983, and 1984, coyote predation on fawns was relatively high during autumn. It may also have been high in some earlier years such as 1961. With the possible exception of 1961, hunter harvests had only negligible impact on fawn mortality.

Over-winter mortality of fawns was important, but quite variable. Of the fawns that died, 26.3% died during winter; however, over-winter mortality rates for individual years ranged up to 82%. Coyote predation was the proximate cause of almost all (95%) of the fawn mortality during winters 1976-1986. Winter severity influenced fawn mortality rates, but not in a simple manner. During most years, fawn mortality increased with winter severity in a density-independent manner (Fig. 6.14). Some years were exceptions, however, and very high mortality occurred in both relatively mild and severe winters, independent of density. Fawn mortality was relatively low, even during severe winters, when microtine populations remained high over winter (1968-69, 1978-79, 1982-83, and 1986-87). In either case, the highest winter fawn mortality rates occurred in years preceded by 1-3 dry summers that resulted in deer entering winter in poor condition. Conversely, moderate fawn mortality during very severe winters was preceded by one or more summers of excellent forage conditions. This occurred when deer densities were both high (1968-69) and low (1978-79). Thus, general body condition and level of fat reserves as affected by summer and autumn forage conditions, winter severity, coyote and alternate prey population levels, all interacted to influence winter mortality rates.

Fawn mortality rates were not significantly correlated with coyote density, but other factors, including forage conditions, winter severity, and population levels of alternate prey were related to fawn mortality rates. Such other factors, at the least, influenced predation rates. This indicated that coyotes and predation, although important, probably were not always the ultimate or overriding factor in fawn recruitment or population dynamics and regulation. Rather, the role and importance of predation was tied to other biological and environmental factors which simultaneously influenced recruitment and numbers of deer on the area.

Fawn survival to early winter was closely correlated with forage production during most years. Because deer density did not affect that relationship, forage quality (defined as the succulence of vegetation) and the timing and length of the period when green, succulent forage was available appeared to be the controlling factor. Calculations of the quantity of forage available, information on antler size and quality among

yearling males, and the lack of density relationships involving antler size also supported that interpretation. All of this indicated that fawn survival/mortality was functionally determined by factors influencing forage quality and the physical condition of deer during fawning and fawn-rearing.

How does the relationship between forage quality and fawn survival to winter reconcile with the fact that 85% of the summer-fall mortality resulted from predation? Were, as some other studies suggest, deer in poorer condition and more susceptible to predation when forage quality was low? Although there may be basis for such supposition, our data indicated that the relationship between deer condition, coyote predation, and fawn survival was not simply one of cause and effect, especially for young fawns.

Regular observations of fawns during summer, including those killed by coyotes, indicated that few, if any were in obviously poor condition. The only exception occurred in 1984, when several fawns, including 2 abandoned by their dams, appeared to be in relatively poor condition at the time of capture. Most other radio-collared fawns killed by coyotes appeared in sufficiently good condition to have survived in the absence of predation; all were active and playful in interactions with each other and their mother when last observed. Moreover, measurements and general observations of deer condition during the years 1973-1977, when fawn mortality was consistently high, indicated that all deer were in at least average, and probably excellent physical condition. They certainly were in better condition during those years than during 1984 and 1985 when some reduction in reproductive effort occurred.

Although no experiments involving coyote control were conducted on our study area in recent years, studies in other western states during the 1970s (Beasom 1974, Kie et al. 1979, Smith and LeCount 1979, Stout 1982) indicated that predator control increased fawn survival or that fawn survival was higher in predator-free exclosures than in adjacent areas. Such results implied that coyotes killed fawns that were healthy enough to survive in the absence of predation.

We noted earlier (Chapter 3) that coyote control efforts on our study area during the 1950s may have influenced the high fawn survival that occurred even during years of poor forage conditions. Similarly, circumstantial evidence from the Sage Creek area, about 96 km southwest of our study area, indicated that fawn survival might have been higher in the absence of coyote predation during the mid-to-late 1970s. There, poor fawn survival and a population decline similar to that on our study area also occurred during and following the

severe 1971-72 winter (C.R. Watts, unpublished data). In contrast with our study area, however, fawn survival subsequently increased sharply after 1972 to a high of 109 fawns:100 adults in winter 1974-75. We did not observe increased fawn survival until 1978-79 despite good to excellent forage conditions through the period on both areas. The major apparent difference between the areas was that coyote control involving intensive private aerial hunting during winter occurred at Sage Creek; no equivalent control occurred on our study area.

Other data also suggested that coyote predation on deer may have been abnormally high during 1973-1975, especially in relation to forage conditions on the study area. Normally, when data were obtained for all species, annual production and survival of young followed similar trends in mule deer, white-tailed deer, antelope, and elk on the area. For example, survival of young was the highest ever recorded for all 4 species during 1979 and was above average for all during 1986. All species experienced below-average survival of young in 1976, 1977, 1984, and 1985. During 1973-1975, survival of mule deer fawns was much below average each year; survival of whitetail fawns was below average during both years for which data were obtained; and survival of antelope fawns was below average during 1973 and 1974 and average during 1975. In contrast, elk experienced average calf survival in 1973 and above average survival in 1974 and 1975.

Forage production and presumably fawn hiding cover was above average during all 3 years, especially in 1974 and 1975, and density of all species was low. Thus, the only difference between elk and mule deer, white-tailed deer, and antelope must have been related to the relative vulnerability of their young to predation by coyotes. The larger size of elk calves and the tendency of elk to form large nursery groups probably rendered them less susceptible to coyote predation.

There was some evidence that non-density-related forage deficiencies can contribute to the intensity of coyote predation on fawns. Forage-vegetation conditions appeared to influence behavioral patterns of deer and the vulnerability of fawns to predation. They also influenced coyote behavior with respect to predation on deer, especially through their effects on alternate prey populations.

Coyotes hunt deer primarily by sight, and it usually is necessary for them to maintain visual contact with the deer to successfully complete a kill. Because of this and the tendency of fawns to remain bedded and well hidden when not nursing during the first few weeks of life (Riley and Dood 1984), most attempts at predation occur after coyotes have observed a fawn active around the doe during nursing bouts

(Hamlin and Schweitzer 1979). The amount of time fawns spend active with the doe increases as they get older. Thus, much mortality of fawns on the area occurred after they passed their most sedentary and cryptic stage (Dood 1978, Riley 1982, Hamlin et al. 1984).

General observations suggested that annual forage conditions and the timing of forage desiccation influenced the degree of coyote predation on fawns by altering activity patterns of both females and fawns. For example, it appeared that during dry years, females spent more time foraging away from their fawn and may have produced less milk (Rowland 1944, Thomson and Thomson 1953) because of difficulty in locating succulent forage. At the same time, hungry fawns spent more time foraging on their own, exposing themselves to observation and attack by coyotes.

Fawns normally spend some time foraging on their own during all summers, and most are at least somewhat active independent of the dam by about 1 August (Riley 1982). Observations during the dry summers of 1983, 1984, and 1985 indicated that fawns were more active, independent of their mothers, during the day than in previous years. Similarly, data obtained by Dood (1978) and Riley (1982) indicated that fawns began foraging about 1-2 weeks earlier during the relatively dry summers of 1977 and 1980 than during 1976, 1978, and 1979. Fawns were born about 6 days later, on average during 1977 and 1980 than during 1979, further indicating abnormally advanced, independent foraging by younger fawns during those dry years. These observations would seem to justify the hypothesis that dry conditions resulting in early desiccation and reduced quality of forage result in behavioral changes in fawns that increase their susceptibility to predation. Such a hypothesis can explain at least some of the interaction between fawn mortality, forage quality, and coyote predation rates; however, more extensive data on fawn behavior during wet and dry summers and relationships to predation rate are needed.

Because coyotes are facultative rather than obligatory predators on deer, alternate prey population levels also played a major role in the relationship between forage production and fawn mortality. Microtine population irruptions coincided with years of high forage production and abundant ground cover. The availability of abundant, easily captured prey and its increased use as food by coyotes (Hamlin et al. 1984) greatly reduced the intensity of coyote predation on mule deer fawns during those years. The fact that fawn survival during 1980 and 1981 was higher than expected based on both forage conditions and microtine population levels, probably reflected increased availability of deer mice and lagomorphs during those years. Both of these groups were more

abundant during 1980 and 1981 than during the previous, 1976-1977 low in microtine populations.

Quantitative data on small mammal populations on the study area were not collected prior to 1976, but data existed from other studies in central Montana (Cada 1968, Tschache 1970, Reichelt unpubl.). Also, qualitative information from a variety of sources such as narratives of game range personnel (Appendix D), annual reports of various individuals and agencies, area newspapers, and field notes provided basis for estimating probable trends in abundance back to the 1930s. Murie's (1935) notations, for example, indicate that both jackrabbits and microtines had probably reached simultaneous peaks around 1932 or 1933. Thereafter the narratives indicated peaks in jackrabbit populations at 10-12 year intervals (early 1930s, early 1940s, 1949-1950, late 1950s, and 1970-1971). Lows generally were noted near the middle years of each decade; ca. 1945, 1955-1957, 1965-1966, and 1973-1977. Our data indicated a subsequent peak in 1983 and a low during 1985-1987. Microtine population highs can be documented during 1963-64, 1968-69, 1978-79, 1982-83, and 1986-87. Moderately high numbers apparently occurred during 1974-75, but the irruption was much less distinct and the peak lower than in 1978-79. Information on deer mouse populations was less complete, but highs apparently occurred in central Montana in 1968 and 1973. Populations on the study area increased from lows during 1977 to a peak in 1983, crashed abruptly in 1984, and subsequently increased through 1986.

Although microtine populations apparently began to increase in summer 1974 and were moderately high during early 1975, fawn survival was poor in contrast to other periods of microtine abundance. However, because the microtines never became exceptionally abundant and deer mice and lagomorph populations, especially jackrabbits, were at cyclic lows during 1973-1977, the combined small mammal prey base was relatively low and did not deter predation on deer.

Some coyote control using compound 1080 was practiced on the area until 1972, although the extent and intensity of efforts was considerably reduced from the late 1940s and 1950s. Narrative reports and field notes indicated that poison bait stations became less effective after the early-mid 1950s when coyotes either learned to avoid the stations and/or poisoning selected for survival of individuals that killed, rather than scavenged for food. Thus, despite at least some effort at control and additional mortality to hunting and trapping, coyotes were common, if not abundant on the area through the 1960s and into the early 1970s. A peak in coyote numbers may have occurred in 1973 as a result of simultaneous peaks in microtine and jackrabbit populations during 1969-1971 and high overwinter mortality of deer in 1971-72. Such a peak

in the coyote population, apparently in response to an abundance of food, was also documented during 1984 (Fig. 5.12), following peaks in microtine and jackrabbit populations in 1982-1983 and high overwinter mortality of deer during 1983-84. Although coyote numbers declined during 1974-1977, they apparently remained sufficiently abundant during 1973-1975 to put extra predation pressure on deer despite the minor peak in microtines during 1974-75.

Our interpretation of the apparent unusually heavy impact of coyote predation on the low deer populations of 1972-1977 may be similar to the relationship described by Gasaway et al. (1983) for wolf and caribou (*Rangifer tardandus*) populations in Alaska. That is, the effects of predation may be inversely density dependent and, when combined with harvests (predation by humans), may maintain deer populations at low levels unless or until environmental conditions change significantly. Similar observations were reported for wildebeest and their predators in Kruger Park, South Africa (Smuts 1978, Walker and Noy-Meir 1979).

Collectively, trends in fawn survival relative to vegetation conditions, coyote and alternate prey populations, and winter severity for the period 1960-1975 indicate similar interactions of all factors on fawn mortality as previously described for the period of intensive studies (1976-1987, Chapter 5). Thus, interpretation of the role and importance of any single environmental factor on fawn mortality and recruitment on our study area and similar environments cannot be determined independently of all others.

Although relative body condition of deer may influence coyote predation rates on fawns, not all deer killed by coyotes were in noticeably poor condition, and even many of those killed when in relatively poor condition might have survived in the absence of predation. Several factors other than body condition and alternate prey population levels were involved in coyote predation on deer during winter. For example, both deer behavior, based on age and experience, and local environmental and site conditions played a role.

Observations of coyotes attempting to prey on deer as well as observations of deer behavior during drive-trapping indicated that, under pressure, fawns are the most likely of all deer to either break away from the group or to stop and stand in confusion. This behavior was also noted by Griffith (1988). Thus, although fawns are generally in somewhat poorer condition than most other deer during any year (Runge and Wobeser 1975, Dusek 1987), it is often their behavior when attacked that makes them vulnerable to predation. Deer in relatively poor condition may tire sooner and stop or break away from a group, but fawns exhibited this behavior even

during years when they were in relatively good condition. Inexperienced behavior might also explain the relatively high predation rate we observed for yearlings as compared with older deer.

Many deer killed by coyotes were found on ice along the Missouri River or Fort Peck Reservoir, but many were also found in uplands. The incidence of coyote kills on the river and reservoir apparently peaked in the mid 1970s, because relatively fewer remains of deer were found on those sites after 1976. Most upland kill-sites were located at the base of steep slopes and in sharply cut drainage bottoms. Evidence indicated that the kills were usually accomplished when the deer fell down on the steep, icy slope or bottom. Snowfall followed by periods of melting and severe cold that caused ice to form on those sites often preceded abnormally severe predation on deer (Knowles 1976 and personal observations). These conditions could cause the fall and perhaps injury of any running deer. Often, when investigating these kill sites, we had to use hand-holds on shrubs to move across the slope.

Because the deer apparently were in relatively good condition, the high losses during winter 1975-76 (Knowles 1976) appeared to be related to icy conditions that prevailed as well as the low alternate prey populations that year. Similar icy conditions prevailed during the relatively mild winters of 1983-84 and 1984-85. Despite poor body condition and relatively high mortality, most deer survived both of those winters in worse physical condition than many deer killed by coyotes in other years. Similarly, Shaller (1967) reported that predation by tigers... "is not confined to the young, old, sick, and surplus animals, but that prime ones are also readily taken". He also pointed out that the method of hunting is less important in determining the class of animals killed than the characteristics of the prey population.

Mortality of Adult Females

Hunting was the major known cause of death among adult females. Coyote predation ranked second among known causes and was suspected to be at least the proximal factor in most mortality for which cause was undetermined.

Most hunting mortality of adult females apparently was additive to other mortality. During 13 years (1960-1972) with a hunter bag limit of 2 deer of either sex, total annual mortality averaged 22.2% for adult females. For 6 years with a 1 deer, either sex, bag limit (plus a very small number of second tags during 4 years), the average was 17%. During 8 years in which only males were legal (except for 0.08 and 0.16 antlerless tags/mi^2 during 1985 and 1986), average annual mortality of adult females was 7.2%. During these same

periods, winter mortality of adult females averaged 6.8%, 6.1%, and 5.4%, respectively. Averaged over long periods, hunting mortality increased average annual mortality, but did not result in a "compensatory" reduction in winter mortality rates. A plot of natural mortality rate against hunting mortality rate for individual years (Anderson and Burnham 1976) did not indicate decreasing natural mortality with increasing hunting mortality for adult females (Fig. 11.1A).

These findings appeared contrary to current concepts concerning compensatory mortality in deer, which hold: 1) that harvest removes animals that would otherwise die from another cause; and 2) that harvest removal of any animal from a population increases the chance of survival (reduces mortality) of remaining animals and/or those of a subsequent cohort in a density-dependent manner. Because of this, it seems essential to further examine both concepts as they apply to mortality patterns and rates of adult females.

It is possible that the low average natural mortality rate of adult female mule deer on the area ($\bar{X}$ = 7.2% with no hunting) allowed little opportunity for compensation to occur. Most work supporting the concept that harvests remove animals that would otherwise die has involved species populations like birds that commonly experience natural mortality rates of 50% or more per year. If a relatively low percentage of all adult females is destined to die over winter ($\bar{X}$ = 6.2% in this study), and those most likely to die are not selected for or against by hunters, only 6.2% of the hunter harvest can be "compensatory" (substitute for natural loss). The remainder, or more than 9 of every 10 adult females shot on the average, is additive and will contribute toward a decline in the population. Thus, annual survival of adult females declined in an almost straight line with hunting mortality rate (Fig. 11.1B).

Overwinter mortality rates may vary considerably (0.7-24.8% during 1960-1986), however, such that the exact degree to which harvest losses in any given year may substitute (be "compensatory") or be additive will also vary. It also may depend on a number of other variables, including the age structure of the adult female segment of the population. The apparent higher harvest rate for older (8.5 +) females than younger females may indicate a slightly greater average degree of substitution than 6.2% for that segment or for the female population in years when animals in that age group are relatively common. Somewhat greater than average compensation could also occur when emigration of yearling females during some years is taken into account. Vacant home ranges of some harvested adult females could be occupied by yearling females which might otherwise have left the population.

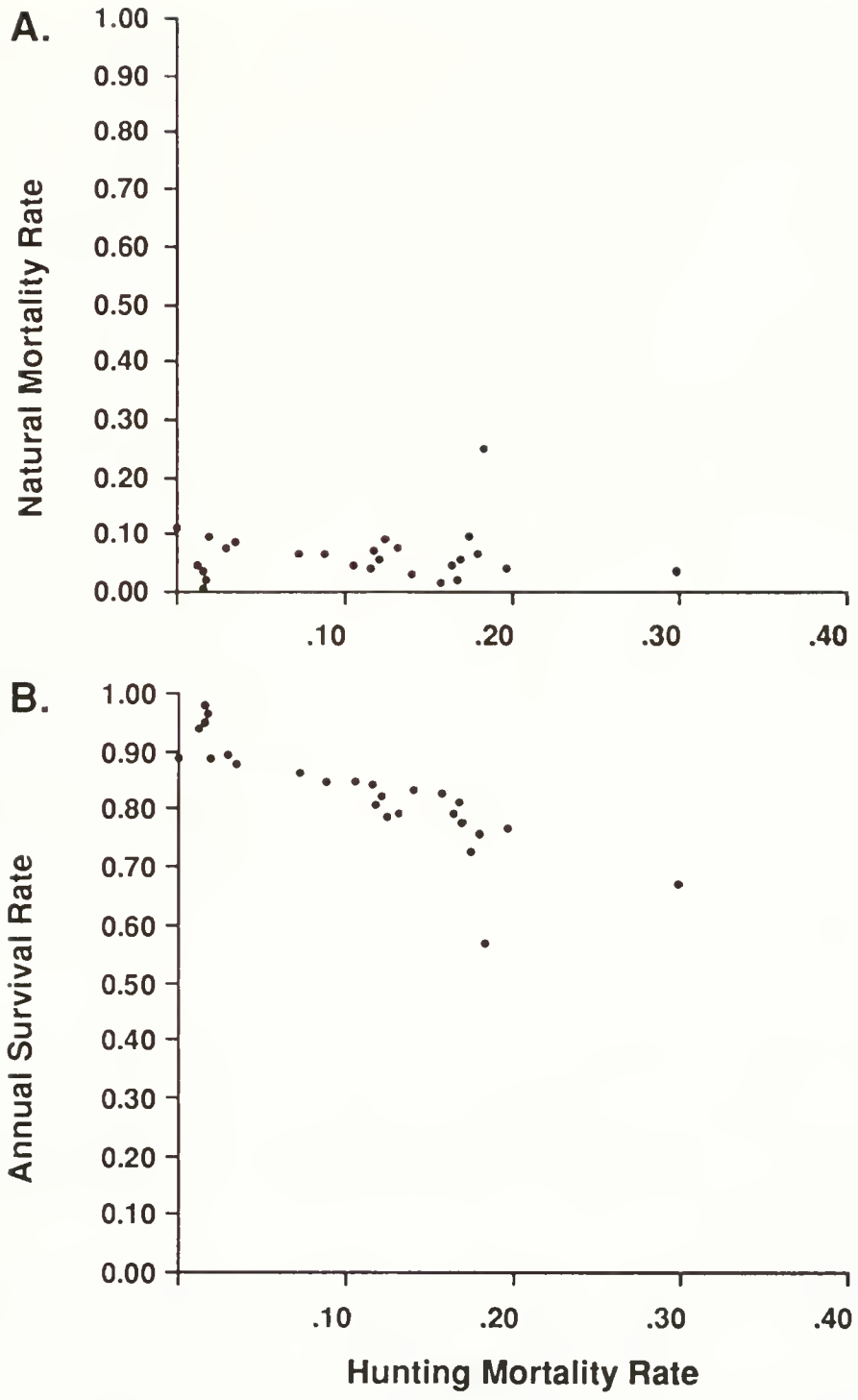


Figure 11.1. A. Annual natural mortality rate of adult female mule deer plotted against their annual hunting mortality rate. B. Annual survival rate of adult female mule deer plotted against their annual hunting mortality rate.

The lack of a relationship between deer density (across the range of densities we observed) and mortality rates may be another reason that there was little evidence of compensatory mortality among adult females. Over-winter mortality of adult females was not significantly related to either total number of deer ($r=0.03$, $P>0.50$, $df=27$) or total number of adult females ($r=0.08$, $P>0.50$, $df=25$) entering winter. It also was not related to the number of adult females in the population the previous summer($r=0.15$, $P=0.47$, $df=27$).

Increased survival of deer remaining after harvest is most often based on the assumption that winter forage is in short supply and limiting deer numbers. It also assumes that harvesting deer prior to winter increases the quantity of forage available per capita for remaining deer, thereby increasing their condition and survival. If winter forage supplies are not limiting, as in this study, neither assumption holds, and much of the rationale for compensatory mortality is gone. Although it may also be argued that reducing deer numbers through hunting could increase per capita forage during other times of the year, we also found no evidence that the quantity of forage during other seasons was limiting, nor that mortality responded to deer density at any time of the year, or in a delayed manner. To clear up possible objections or confusion over terms, we note here that we have already (Chapter 5, earlier discussion this chapter) indicated that we had no evidence for density-dependent compensatory reproduction. Thus, hunting mortality of adult females resulted in little substitution (compensatory mortality), no measurable decrease in mortality as the result of increased per capita forage, and no compensatory reproduction.

Although hunting mortality was a major cause of mortality for adult females, hunting mortality rates were low to moderate, and generally below long-term average recruitment rates. Only during 1961, 1964, 1971-74, and 1984 was hunting mortality of adult females, by itself, greater than subsequent recruitment. During those years, however, recruitment was much below average.

A stable population can be maintained with some adult mortality in all years because at least some fawn recruitment always occurs. In some years, however, the natural mortality rate among adult females was higher than recruitment. Thus, the availability of a "harvestable surplus" of adult females varies among years. It could also vary with management goals; i.e, to increase, stabilize, or decrease numbers of deer in the population. The ease with which harvest can decrease population size during years or periods of low recruitment and/or high adult mortality was demonstrated by population trends during 1961-1962 and 1972-1974.

Exceptionally heavy harvest of adult females and fawns in connection with low overall fawn recruitment in 1961-62 resulted in a sharp, though relatively modest population decrease to winter, spring, and summer 1962. Despite a subsequent reduction in the harvest, continued low recruitment resulted in stabilization of population size to the following winter-spring and provided the base for population increase and a larger "surplus" in 1963 when good recruitment occurred.

The combined effects of low fawn recruitment, severe winter mortality, high overwinter mortality of adult females, and relatively high harvest mortality of adult females resulted in a very sharp and substantial decrease in both total population size and the adult female population from autumn 1971 to spring and summer 1972. Continued liberal harvests of adult females along with low fawn recruitment influenced further reductions in total population and adult females through 1974. Overwinter mortality of adult females was relatively low (5-10%) in each of those 3 years. However low recruitment and a female age structure comprised primarily of individuals with a very low natural mortality rate (susceptible females were eliminated during the severe 1971-72 winter), essentially precluded any "harvestable surplus" throughout the period. Under those circumstances, all mortality was "additive" and reduced the female population. Such a low population level was reached that the absolute number of fawns recruited was insufficient to stabilize or increase population size. It was not until 1978, when fawn recruitment increased as a result of decreased coyote predation, that the population could begin to recover.

The potential for a similar impact of hunting existed during 1964-1965, when severe winter conditions also occurred. Although fawn mortality was heavy during the 1964-65 winter, adult female mortality was relatively low. Harvest mortality of adult females was also relatively low in autumn 1964. Thus, while total deer numbers on the area declined considerably to spring 1965, the decrease in adult female numbers was not extreme. Also, fawn recruitment exceeded adult female harvest rates and was only slightly below total female mortality in 1965 and 1966 so total female numbers remained relatively high and stable until fawn recruitment increased sharply in 1967.

Generally, in this environment, conditions that resulted in below-average fawn recruitment rates also resulted in above-average natural mortality rates among adult females, and vice versa. When recruitment rate is declining and female mortality is increasing, and a management goal is to stabilize or increase numbers of deer, the only option is to curtail hunting mortality of adult females as rapidly as possible. Previously, it was assumed that recruitment was declining and

adult mortality was increasing because of deficiencies in the quantity of deer forage on the area. Thus, further reduction in deer numbers by continued heavy hunting (as occurred during 1972-74) should have improved forage conditions at least on a per capita basis and resulted in compensatory increases in recruitment and decreased natural mortality. Our data indicate that neither occurred to a significant degree; rather hunting mortality was mostly additive to other mortality, and served to further reduce the population.

Although predation rates were generally low for adult females, predation was the second most common cause of mortality for adult females. Most coyote predation on adult females occurred during winter and spring; though at least some occurred during summer and autumn. Over-winter mortality for adult females, from all sources, was usually less than 10%, exceeding that level only during 1971-72 (24.8%) and 1975-76 (11.3%). Even if all winter mortality was the result of coyote predation, its impact normally would be relatively low. However, over-winter mortality and predation rates of more than 5% on adult females, although by itself not of great impact, indicated that mortality and predation rates for fawns were usually high and that recruitment would be low.

Adult females in both relatively good and relatively poor condition were killed by coyotes. Those in poor condition may have died in the absence of coyote predation and their loss may have substituted for other mortality. Most of the adult females killed by coyotes during 1975-80 were in relatively good condition. They probably would not have died in the absence of coyote predation and their deaths probably helped contribute to the low, stable populations of the mid-late 1970s. They were certainly in better condition than many females that survived winters 1983-84 and 1984-85.

Both hunting mortality and coyote predation reduced the numbers of adult females, but, during most years, hunting had a greater numerical impact than coyote predation. During years that harvests of antlerless deer were legal, hunting usually removed at least twice and occasionally up to 5 times as many adult females from the population as other sources of mortality. The effect of varying levels of adult female mortality on population numbers depended upon fawn mortality and recruitment rates. Even relatively low mortality rates for adult females contributed to declining or stable populations when recruitment rates were as low as or lower than female mortality rates.

During 1972-1977, because of very low recruitment of fawns (15-55 yearling females/year), even relatively low coyote predation rates on adult females contributed significantly to declining or stable populations. This was

especially true during 1972-74, when losses of adult females to predation were added to hunting mortality. Even at the low densities of 1972-77, compensatory increases in recruitment did not occur.

Mortality of Adult Males

Hunting was the major cause of mortality for adult males; few died from other causes. Harvest rates for adult males averaged 37.5% from 1960-1986, ranging as high as 58%. During the years that marked males were present, composite samples indicated that mortality from hunting averaged 36.4% for yearling males and 53% for males 2 years old and older. Sex ratios of adults averaged 42 males:100 females pre-hunting season (range, 20-64:100) and 31 males:100 females post-hunting season (range 13-50:100). Male:100 female ratios for some unhunted deer populations (Martinka 1978, Gavin et al. 1984, Kie and White 1985) were no higher than for this hunted population during many years. Gavin et al. (1984) indicated that the annual mortality rate for adult male Columbian white-tailed deer was 40%, even in the absence of hunting mortality. They suggested that increased energy utilization associated with the breeding season resulted in poor condition of males and subsequent winter mortality. Similar conclusions were made by Flook (1970) to explain the higher natural mortality rate of adult male elk compared to adult female elk in unhunted populations.

The relatively low rates of winter mortality for adult males in the population during 1960-1986 (3.8%) and for marked males (8.7%) during 1977-1986 (marked sample was older than the male population as a whole, 1977-86), suggested that hunting mortality may be less additive to winter mortality for adult males than for females or fawns. Harvest rates were higher for males than for antlerless deer, so a greater portion of those destined to die over-winter were harvested. The older, dominant males, most likely to be in poorest condition after the breeding season, were also those most heavily harvested by hunters.

During many years, especially those preceding severe winters, lower harvest rates for males might not result in appreciably lower total annual mortality rates. We do not know what the natural mortality rates of adult males are in this population in the absence of hunting, but it is unlikely the annual increase in survival would exactly match the decline in harvest rates. If, in the absence of hunting, annual natural mortality rates of adult males in our population were as high as the 40% observed by Gavin et al. (1984), then the majority of hunting mortality of adult males at current levels (especially that of older males) may not be additive to winter mortality. However, because not all

hunting mortality of males is likely to be compensatory, at least some increase in survival of males should occur following a reduction in harvest rate.

Emigration and Immigration

Relatively high rates of emigration (>50%) occurred among yearling males during all years. Because our data did not indicate annual declines in male populations owing to emigration, yearling males from adjacent areas must have immigrated to the study area in nearly equal numbers to emigrants. Dispersal of yearling males can, thus, be viewed as a mechanism for redistribution of males for genetic interchange and allocating resources by sex, but not as a factor that increases or decreases numbers of yearling males within our study area.

Emigration of yearling females was much more variable and apparently not balanced by immigration. The majority occurred at low population densities, among yearlings in the first 2 numerically large cohorts recruited following the population low in the mid 1970s (those born in 1979 and 1980). Neither emigration nor immigration were detected among marked deer or in population estimates and classifications during years of mid to high population densities (among cohorts born between 1981 and 1985). A probable temporary movement of adults and fawns onto the study area from surrounding prairie during the dry autumn of 1983 was not considered equivalent to permanent immigration or dispersal of yearlings. A few females and their fawns were also observed to temporarily move off the area for a few weeks during some years.

Net emigration apparently also occurred among yearling females born in 1986. One of the 2 radio-collared yearlings on the area in spring 1987 was known to have dispersed to the north off the area; the fate of the other was unknown, but radio contact was lost during the period when dispersal occurs. Although this sample was too small to indicate the degree of dispersal during spring 1987, it did indicate that emigration occurred. Subsequent population estimates not only documented that emigration of yearling females had occurred, but also that it was extensive and involved up to 49% of all females surviving from the 1986 cohort. Overall, about 215 females "disappeared" between spring 1987 and December 1987. About 100 of these could be accounted for as hunting mortalities during autumn 1987, most of the remaining 115 had to have emigrated. Total female density, including all yearlings from the 1986 cohort, was the highest ever recorded ($3.3/km^2$) in spring. Net emigration reduced that to about 2.8 adult females/km^2 by autumn, equivalent to the previous high in 1983.

The available evidence indicated that net emigration of yearling females occurred at the lowest and highest female densities observed during the study, but not at intermediate densities. Considering the small samples of marked yearlings, it was possible that dispersal occurred but was not detected during years of moderate to relatively high female density. However, because female population estimates generally were closely consistent with numbers of yearling females recruited, any emigration that occurred during those years had to have been balanced by immigration.

The observed pattern of emigration among yearling females was similar to the pre-saturation and saturation dispersal proposed by Lidicker (1978). It was not consistent with the "social fence" hypothesis proposed by Hestbeck (1982) in that it did not explain the net emigration at high population density. This inconsistency may be explained by the habitat and social behavior of deer on our study area. The southern, southeastern, and southwestern portions of the area were bounded by blocks of very marginal or non-deer habitat, across which yearlings could disperse and not encounter aggressive "neighboring" deer until they were a significant distance from their natal range. Also, variation in size of social groups apparently depended more on fawn survival than on deer density, and dispersal did not necessarily consist of movement to just the nearest available, open habitat. At both low and high densities, dispersers moved long distances within a day or two, by-passing interaction with close neighbors.

Saturation dispersal (Lidicker 1985), occurs at densities at or above "carrying capacity"; pre-saturation dispersal occurs before "carrying capacity" has been reached. Reasons advanced for pre-saturation dispersal include genetic selection and availability of unfilled habitat. Although it is possible that "habitat fill" was the motivating factor behind dispersal of yearling females at high densities, previous social experience could also explain their dispersal at both low and high densities. Occupation of vacant habitat should not occur at 100% efficiency up to the point of habitat fill. Thus, during all years, at least some animals should not find habitat suitable to establish home ranges until they have passed the study area boundaries. If habitat fill was the only factor motivating emigration at high densities, it would follow that at least some, and probably an increasing amount of emigration would occur as density increased (Lidicker 1978). Similar to Gaines and McClenaghan (1980), we did not find that emigration increased proportionally with density. However, it is possible that more intrapopulation dispersal or small shifts in home range occurred with increasing density.

Past social experience may explain the variation in rates of emigration among yearling females. Petrusewicz (1963) found that experimentally induced disruptions to social structure could result in changes in density of stable laboratory populations of mice. Population growth could be induced by both removal and addition of several new mice to the population. This suggested that different social structures may tolerate different levels of density. Terman (1962, 1963) for deer mice, Calhoun (1963) for Norway rats, and Hunter and Davies (1963) for Scottish blackface sheep have shown that early social experience is important in determining subsequent spacing behavior.

Both periods of high emigration during our study were preceded by at least 2 years of poor fawn recruitment, when few yearling females were added to matrilineal social groups. Under those circumstances, mature females enjoy relative solitude and little social interaction at the time of parturition. A sudden increase in the number of yearlings recruited (spring 1980, 1981, and 1987) could elicit very aggressive behavior by mature females around their parturition territory. On the other hand, after several years of increasing recruitment and the addition of yearling females to social groups during autumn and winter (1981-83), mature females may be more used to the presence of other deer such that yearlings are tolerated nearby as long as they don't approach the new fawn.

Thus, past social experience, as influenced by recruitment of yearling females, could explain both pre-saturation and saturation dispersal. During this study, both periods of dispersal occurred during good forage and weather conditions that followed several years of poor fawn recruitment. These conditions served to enhance the opportunity for success by dispersers (colonizers).

Regardless of the reason for its occurrence, emigration of yearling females reduced the growth rate of the female population during years that it was documented. During 1979-80, net emigration of yearling females reduced the instantaneous growth rate of the female population from 0.353 to 0.258; during 1980-81 the reduction was from 0.262 to 0.212; and during 1986-87 the reduction was from 0.220 to 0.085. Even though many of those yearlings were incorporated into populations occupying adjacent marginal habitats, their loss reflected "mortality" to the mule deer population on our study area.

Overall, emigration did not appear to occur in a manner or to the extent that it would singly control mule deer numbers. Rather, it was one of many factors that at times, reduced populations in core areas below those which would have

occurred based on recruitment rates. Perhaps the most important role of dispersal and emigration was to maintain mule deer in vacant available habitat on and off the study area and maintain genetic diversity.

"Dispersal is increasingly viewed as having significant demographic causes and consequences" in microtines (Lidicker 1985). Observations of the "fence effect" for at least 6 species of *Microtus* is evidence that dispersal prevents or slows population growth as long as a dispersal sink is available (Lidicker 1985). Thus, it is possible that some conclusions regarding the effects of increasing density on reproduction and mortality based on studies of deer in enclosures (Kie et al. 1979, McCullough 1979, Ozoga et al. 1982b) may not be entirely applicable to a natural environment where emigration is not impeded. In most studies of "penned" deer, density reaches much higher levels than observed in adjacent habitat where dispersal could act to keep densities below levels that result in density-related nutritional and social problems affecting reproduction and mortality. Similar conclusions might be made about studies (Verme 1965, 1967, 1969) that "artificially" raise density by decreasing forage quantity and quality of penned deer to levels "seldom encountered by free-ranging whitetails" (Verme 1965).

Klein and Strangaard (1972) observed that food did not appear to directly regulate roe deer (*Capreolus capreolus*) numbers in Denmark through malnutrition or starvation except in situations where areas were fenced. Instead, they indicated that dispersal by young animals kept roe deer populations below densities where forage supplies become a factor in population regulation. However, they also noted that social factors controlling roe deer populations would not apply to North American deer because the latter are not territorial and deer habitats are relatively continuous with no low density areas to absorb the dispersing surplus. We now know that those assumptions were premature. Findings of Ozoga et al. (1982a) and this study indicate that some North American deer can be functionally territorial. Similarly, many North American deer populations, especially in the west, are surrounded or interspersed by marginal or low-density habitat capable of absorbing dispersers. Until recently, the potential impacts of functional territoriality and dispersal have been ignored or underestimated. We suggest these impacts must be further examined and considered in research and management of free-ranging populations.

Interaction of Reproduction and Mortality

Our data (Chapters 5 and 6, Hamlin and Mackie 1987) indicated that a condition cycle in females related to reproduction may contribute to periodic low fawn recruitment

and high adult female mortality. Lactation stress associated with rearing fawns to weaning age may be severe (Short et al. 1969, Clutton-Brock et al. 1982), even during relatively good forage years. Females that have recruited fawns to early winter do not accumulate as much body fat as females that did not have fawns or lost them early. Successfully rearing fawns for 2 successive years or more probably requires drawing on body reserves in addition to the nutrition supplied by current forage.

The cumulative effect of several years of successful fawn recruitment is relatively poor body condition for the female. The "average" decline in fawn production and recruitment rates that we observed after 6 years of age and increase in female mortality between ages 6 and 7 probably reflected this cumulative reproductive stress. Obviously, not every female on the area died between ages 6 and 7 or did not rear a fawn at age 7. Based on the evidence obtained, however, those females which had successfully reared the most fawns prior to 6 years of age were in poorest condition and thus most vulnerable to either death or poor recruitment of fawns thereafter.

The exact age of the female may not be the most critical factor, but rather her reproductive history. On "average", 6-year-old females are most vulnerable, but a 5-year-old female that has recruited fawns for 4 successive years is probably more vulnerable than a 6-year-old female that has only recruited 2 fawns in 5 years.

Prevailing environmental conditions, especially during summer and autumn may be important in these relationships. If a dry summer and/or autumn occurs after 2 to 3 years of above average fawn recruitment for the population, females that rear a fawn to weaning, or close to weaning, during the dry year are often in very poor condition. They may be in too poor of condition to breed or to breed at maximal rates such that initial fawn production declines, as was the case during 1983-84 and 1984-85. Additionally, many females may be in such poor condition that they die over-winter. Thus, because of declining female condition resulting from cumulative reproductive stress, a series of years of high fawn recruitment carries within it the seeds of its own destruction.

Similarly, the older and dominant breeding males, which are most active during the autumn breeding season, are in poorest condition entering winter and are the males most likely to die over-winter (Gavin et al. 1984). Their deaths occur because of excessive energy expenditure immediately prior to winter, not because of intraspecific competition for

forage that is inadequate in quality to increase the condition of any deer.

Physical condition of females can also decline because of reproductive drain unrelated to increased intraspecific competition for food. This scenario can occur even over a long series of years of relatively good forage quality, but is especially likely to occur when a series of good years is followed (as is often the case) by a very bad year. All females are more vulnerable than usual to mortality and low productivity when a very dry year occurs, but those which had been most productive in previous years are most vulnerable. Thus, poor female condition following extended periods of high productivity can explain both the unusually high female mortality that occurred during winters 1964-65, 1971-72, 1983-84, and 1984-85 and the low fawn recruitment observed during the following summers. Fawn recruitment was generally high to weaning during the prior years of 1963-64, 1967-70, and 1977-83, respectively.

Often, recruitment remained relatively high during the first year of poor forage following good years. That occurred because, when current forage conditions were not extremely bad, females can rear 1 more fawn crop by utilizing body reserves. This, however, only leads to further deterioration in body condition, even poorer fawn recruitment, and increased adult female mortality the following year.

Although superficially, these condition cycles often appeared to coincide with changes in density, density and intraspecific competition for food were not the operative factors. Physical condition of females that successfully recruited fawns declined even during what were considered good forage quality years with low deer density on our study area. A decline in recruitment, often drastic, is triggered by a cumulative decline in female condition and/or an abrupt change in forage quality unrelated to an increase in deer density. Condition cycles in adult females are more related to density-independent changes in quality of forage and cumulative fawn recruitment rates than to deer density and forage quantity.

Increases in deer density result because fawn survival increases and adult mortality decreases relative to previous levels. Random variation of environmental conditions can result in patterns of fawn recruitment that will mimic what has been viewed as density-dependent recruitment. By random chance, a good fawn recruitment year or series of years is most likely to be followed by at least 1 year somewhat worse than the good year(s). Fawn-rearing conditions can vary considerably across a spectrum, but generally fall within certain limits, depending on environmental variation in the area. Extremely wide environmental fluctuation does not

increase variability in fawn recruitment beyond certain finite mathematical and biological limits. Fawn recruitment cannot be less than zero no matter how bad the year and practically cannot be higher than about 1.8 fawns per 2-year-old and older female, no matter how good the conditions. Because of those considerations, we can place fawn-rearing conditions and recruitment levels into limited categories.

If forage quality and fawn-rearing years are rated on a scale of 1-10, with 10 being the best and 1 the worst, we can illustrate scenarios indicating that random variation can mimic properties of density-dependence. For example, at the most extreme end, a year that was at the best level for fawn-rearing and recruitment (10) can only be followed by a year that is equal to it (10) or worse (1-9). Random chance dictates that the year following the best year will usually (90% probability) be worse. If year A was an 8 for fawn-rearing conditions, or years A and B were 9 and 8, by random chance the next year is more likely to be worse (1-7, 70%) than equal or better (8-10, 30%). Random environmental variation can lead, over time, to any possible successive combination of years, but regression to the mean and random chance dictate that, on average, relatively poorer fawn-rearing years will follow relatively good fawn-rearing years and vice versa. Thus, it will appear than an increase in deer density (resulting from good years) is followed by a decrease in recruitment. Also, the increase in non-productive yearlings automatically lowers population recruitment rates to some extent. Alternatively, a year or 2 of good fawn recruitment often follows several years of declining deer density (resulting from poor recruitment). When observed over the short-term, these scenarios appear to represent density-dependent fawn recruitment. The same scenarios, however, can result from randomly varying environmental conditions and regression to the mean.

Any data purporting to prove density-dependent relationships must show that it occurs to a greater or more precise degree than would appear to occur because of random variation. Longer-term studies can place this phenomena in perspective and indicate, at least on this area, that similar levels of increases and of decreases in recruitment occurred over a wide range of densities. The importance of long-term studies (20 years +) in interpretation of cause and effect can be illustrated by our data. A study on our area starting in 1973 and continuing for 7 years (through 1979) would have indicated that fawn survival <u>increased</u> as density increased (Fig. 11.2). We do not mean to imply here that fawn survival does increase with density, only that it is not necessarily related to density. Most wildlife/population ecologists consider 7 years to be a long-term study. Certainly most published studies, including most indicating support for

density-dependent regulation are shorter than 7 years. Only recently have studies of adequate length been available that properly question existing concepts.

In the Breaks environment, the physical condition of females declined with age and following several years of above average recruitment rates, regardless of forage conditions. We found no evidence that intraspecific competition for forage played a major role in that condition cycle. Reduced initial reproductive effort and poor survival of the subsequent fawn crop often go hand-in-hand because of the female condition cycle and because, on average, poor forage years tend to follow good forage years. Obviously, those females attempting to recruit fawns during periods of poor forage conditions will be in worse physical condition than during times of good forage conditions, but body condition for productive females declines even during good forage years if they rear fawns. On the other hand, females that do not rear fawns and do not undergo lactation stress can maintain and often even improve body condition during relatively poor forage years. The length of winter through its effect on plant dormancy and the severity of winter through its effect on energy expenditure also affected deer condition and the interaction of reproduction and mortality.

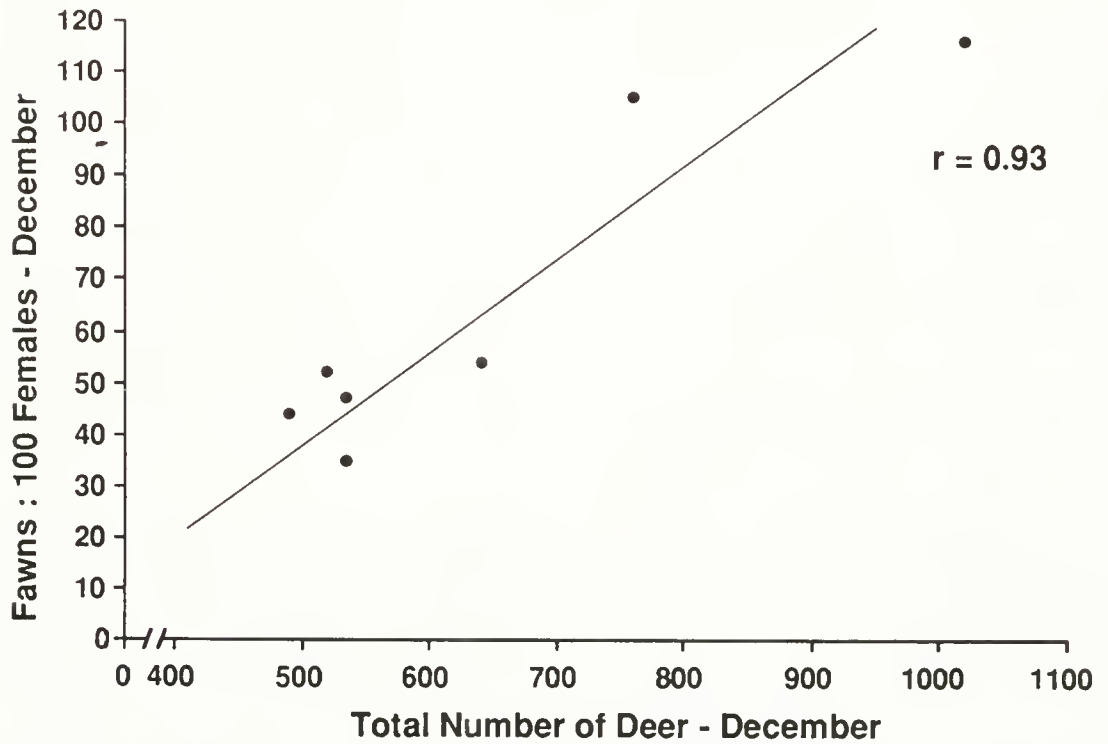


Figure 11.2. Fawns observed per 100 females during December plotted against the total number of mule deer in the population during December, 1973-1979.

To summarize, then, many different factors influenced and/or interacted to influence fawn production and recruitment and adult mortality. Summer forage condition, especially forage quality as determined by the availability of succulent green vegetation during spring and summer, was extremely important. Forage quantity was generally adequate during all seasons and only incidentally related to population performance. Both forage quantity and quality appeared to be controlled primarily by climatic variation and succession; deer densities and grazing or browsing by deer had no detectable effect.

Climatic factors also determined the timing and length of periods of both positive and negative energy balance. Weather conditions, especially precipitation received during the 9 months prior to initiation of plant growth and temperature during the growing season, determined total forage production and length of time that forage plants remained succulent and provided quality forage. During some years, heavy late summer or early autumn rains result in an autumn "green-up," prolonging the period of positive energy balance. Weather factors influencing variability of onset and end of winter and severity of winter all affected the length and severity of the period of negative energy balance. Forage conditions from spring through autumn, together with current and past history of lactation stress, established the condition of the female entering winter. The consequence of the condition in which deer enter winter during any particular year depends on the length and severity of the winter period. Length and severity act together, but length acts primarily in determining how long deer must use maintenance quality or poorer forage, whereas severity determines the degree of energy deficit relative to available forage and fat reserves. Possible summer-winter energy balance combinations are as variable as the weather. In one sense, net recruitment of deer to the population is the result of a net annual positive energy balance, and net deaths in the population are the result of a net annual negative energy balance.

Predation rates on mule deer by coyotes appeared to be closely related to cycles in microtine rodent and lagomorph populations, which served to buffer predation on deer during periods of relative abundance. However, high prey populations may also result in high coyote populations that persist for a year or 2 after the "crash" of the small mammals. Within those underlying cycles, the exact level of lows and highs in alternate prey populations is probably set by forage/cover conditions influenced by climatic variation. In addition, the level of coyote predation during winter can be influenced by variable snow and ice conditions that determine accessibility

of alternate prey and create advantageous hunting and killing conditions for coyotes preying on deer.

Net emigration of yearling females during some years, although enhancing adjacent populations in marginal habitat, resulted in "mortality" or reduced recruitment to the female population on the study area. Induced primarily by behavioral factors, emigration may act periodically as a natural population regulating mechanism by reducing population growth rate following several years of low fawn survival at either low or high female densities. Overall, however, it did not appear to be of singular importance in limiting numbers and the population dynamics of mule deer on the area. Rather, dispersal in the early years of increase following population declines or lows may benefit recovery by rapidly refilling vacant habitats capable of sustaining and producing deer during periods of favorable environmental conditions, both on and off of the study area. This, at high densities, may also serve to maintain deer in more marginal habitats during years of good conditions.

Considering all other factors affecting the population, hunter harvests that were not adjusted to periodically low recruitment and increased natural adult mortality rates directly reduced the population and influenced trends and dynamics over periods of one to several years. Although hunting generally did not significantly influence fawn recruitment rates, its role in reducing the number of adult females on the area, in conjunction with other mortality factors, did influence absolute numbers of fawns/yearlings recruited and, thus, also population trends during some periods. The fact that hunting mortality, especially among adult females, was largely additive to other mortality indicated that hunting can be an important regulatory factor or mechanism in the population at times. However, its overall effect in determining trends through the years was minimal relative to environmental variation.

Although any attempt to model the role or importance of various single factors on the population is unrealistic, considering all interactions involved, it may be somewhat indicative of the relative contribution of some factors to trends we observed. For example, for 7 years from December 1980 through December 1987, the population increased from 1,175 to 1,405 mule deer, though not in a straight-line manner (Fig. 4.2). Despite this growth, many "potential" deer were lost to the population.

If no mortality other than a few deaths from accidents and old age had occurred and reproduction had been at the maximum observed rate each year, simple arithmetic modeling shows that the population could have increased to 38,840 deer

at the end of 7 years. Coincidentally, this is also an average annual growth rate of r=0.50, equivalent to the maximum expected for the population (see Chapter 4). By additional "modeling," we can compare the relative contribution of each of several major mortality factors in limiting population growth from the potential to that actually realized.

If no emigration of yearling females had taken place during 1980-1987, but all other mortality factors had operated at rates observed annually, the mule deer population would have been 1,725 in December 1987 (1.23 times greater). If reproduction had occurred each year at the maximum observed rate, but all mortality factors had remained as observed, the population would have reached 1,780 deer in 1987 (1.27 times greater). Similarly, assuming that all other mortality factors operated at observed rates, if there had been no hunting mortality of antlerless deer, the population would have reached 2,155 deer in December 1987 (1.53 times greater). With no hunting of any deer, it could have reached 2,940 (2.09 times greater). With no coyote predation on any deer, it should have reached 9,540. Although coyote predation was the proximal cause of loss of most of the potential, and in its absence the population could have been 6.8 times higher in 1987 than actually observed, the interaction of all factors was even more important. Without all factors interacting, the population would have been 27.6 times higher than actually occurred.

Obviously, all other mortality rates would not have remained the same if any factor had been eliminated. The elimination of even the factor with the least influence, emigration, would have resulted in higher populations in December than we ever observed on the area. Thus, results equivalent to "penned" deer studies may have occurred, and at higher population levels, we may have observed density-related effects on reproduction and mortality. The important implication is that the combination of all factors (multi-factorial approach, Lidicker 1988) apparently has kept the population below levels where density-dependent mortality is easily observable. Probably, no 1 factor can be said to regulate the population unless we call the total variable environment 1 factor.

CHAPTER 12

POPULATION REGULATION

Thus far, we have discussed what the population did, how it did it, and to a limited extent, why it did what it did. We now concentrate more fully on the latter and the questions of why the population behaved in the observed fashion, why abundance varies from place to place, and why no population increases without limit (fluctuates). In the context of population ecology these are the essence of population regulation or limitation.

The population we studied displayed an initial growth pattern (Fig. 4.7) that was similar to a "typical" logistic growth curve, implying density-dependent processes. Indeed, the entire pattern of population growth and fluctuation (Fig. 4.7) appears similar to countless growth patterns displayed in articles and texts as representative of density-dependent regulation. The key point, however, is that almost all the theoretical work focuses on the initial "irruptive", logistic growth phase. Subsequent fluctuations, if considered at all, are passed off lightly as "minor" fluctuations about "carrying capacity" (K). Seemingly, it is assumed that similar processes operate within these fluctuations as within the initial growth phase.

Our data collection and mathematical tests occurred entirely within the fluctuating phase of an established population. What may be termed minor fluctuation by theorists or mathematical ecologists is of major concern to population managers. During 1972-77, for example, neither deer managers nor hunters in eastern Montana were pleased with ongoing "minor" fluctuations in mule deer numbers. Compensatory reproduction and mortality (density-dependent processes) were nowhere evident. Thus, the question was not what processes operate in founding populations, but what determines fluctuations of established populations. Fluctuations in established populations might not result from density-dependent regulation. If that is so, the implications to management are entirely different than those inherent in density-dependent regulation theory.

Factors regulating populations can generally be placed into 2 categories; intrinsic and extrinsic, though there are variations and combinations (see Chapter 1). Proponents of population regulation by intrinsic factors or processes hold that there is self-regulation by the population that prevents it from reaching densities where it harms or destroys its resource base. Various intrinsic mechanisms, operating in a variety of ways have been proposed--behavior, physiological change, genetic selection. All key on population density as

the triggering cue and thus, all are variations of density-dependent population regulation.

We could find no evidence to support the theory of self-regulation by populations. Mule deer on our study area employed a range of intrinsic behavioral and physiological mechanisms to deal with the variability of extrinsic factors. Variable emigration, food habits and habitat use, and movement strategies were all examples of such mechanisms. However, these intrinsic mechanisms by themselves, did not function to regulate population growth. Rather, they dampened the effects of variable extrinsic factors. Thus, population growth was not as fast nor decline as severe as might have been the case in their absence.

It was also unnecessary to invoke intrinsic mechanisms to explain major changes in the population. Behavior that contributed toward slowing population growth (parturition territoriality and emigration) occurred at all densities and did not halt population growth. A condition cycle (another possible intrinsic factor??) that explained some variations in reproduction and mortality was influenced to a large extent by variable weather (an extrinsic factor). Our conclusion is that intrinsic mechanisms interacted with extrinsic factors to moderate population growth and decline, but did not directly regulate population growth.

The role and importance of extrinsic factors in regulating or limiting population growth has received the greatest attention from population biologists. Various extrinsic factors (e.g., weather, food, space, predators) have been suggested to regulate populations in either a density-dependent or density-independent manner, or both. Regulation by resource shortages (especially food) through density-dependent feedback (Nicholson 1933) is widely accepted. However, limitation of population growth through density-independent changes in weather (Andrewartha and Birch 1954) also has its adherents.

We found that weather affected the deer population in various ways, both directly and through influence on other extrinsic factors such as food, space, and predation. Our data clearly showed that fawn recruitment was directly influenced by forage conditions (see Chapter 5). Through a delayed condition cycle, adult mortality was also influenced by forage conditions. We found no evidence, however, that forage production, availability, or conditions were substantially influenced by deer density. Thus, we also found no evidence for population regulation through a density-dependent feedback loop. Rather, the primary influence on forage conditions was density-independent changes in weather. This finding is strongly emphasized because it is a major

departure from the explicit or implicit assumptions in density-dependent theory that the number of animals grazing or browsing is a primary factor influencing forage production and quality.

The influence of weather on vegetation production also influenced cover for deer and forage and cover for alternate prey (microtines and rabbits), thereby influencing coyote predation rates and deer mortality. Predation rates were also influenced by variable snow and ice conditions. Weather also influenced the energy balance equation of deer both through forage production, quality, and availability and through its influence on energy demand by deer.

Through interaction with the fixed habitat base, weather (wind, snow depth, forage quantity and quality) affected the kinds (reproductive, non-reproductive, long-term, temporary) and amounts of effective deer habitat (space). Deep, drifted snow resulted in some areas becoming non-habitat (nutritionally, excessive energy use, vulnerability to predation) during some winters. Similarly, during drought, some areas could not provide even maintenance quality forage, or their use required behavioral changes in deer that increased their vulnerability to predation.

Because of the pattern of deer dispersion at habitat fill, more deer occupied marginal areas at high than at low densities. Thus, mortality could be high at high densities (density-related) under certain weather conditions. However, this relationship was not deterministic or consistent. When weather conditions remained favorable, mortality was low even at high densities.

Overall, the variable weather, interacting with the fixed habitat base was the most important factor influencing the deer population. This occurred because weather also influenced all other factors including food, energy demand, predation, available habitat (space), and even hunter harvest. Within limits of the fixed habitat base, population growth was limited by the time that weather conditions were favorable and population decline was limited by the length of time that weather conditions were unfavorable.

The role and importance to population dynamics of proximate factors such as predation and hunter harvests has been discussed earlier (Chapters 5, 6, and 11). Coyote predation was the major proximal cause of deer mortality. Although, it appeared that predation often functioned as an agent of variable weather, the absence of predators would probably result in at least temporarily higher deer densities. At these higher densities, it is possible that density-dependent effects on reproduction and mortality might be more

observable. Because hunter harvest may be extraneous to the development of "natural" regulation of populations, it will not be discussed here. However, hunter harvest is the major factor we can control or manage and will be further discussed in Chapter 13-Management Implications.

The finding that variable weather is the major factor influencing forage production and quality and population dynamics of herbivores is not new (Talbot and Talbot 1963, Teer et al. 1965, du Plessis 1972, Hirst 1975, Sinclair 1977, Medin and Anderson 1979, Croze et al. 1981, and Rogers 1987) However, the tendency has been to assume almost perfect operation of density-dependent reproduction and mortality despite non-density related changes in forage conditions. Under this assumption, reduction in density always increases nutritional level and survival. In contrast, we maintain that under unfavorable conditions the condition and fates of individual animals vary as individuals, not as 1/N. Thus, during drought, a reduction of density by one-half as a result of harvest does not mean that the remaining animals will all survive because they now have twice as much to eat. In some drought situations, <u>any</u> surviving animals have only sub-maintenance quality of forage to subsist on and quantity is not important.

A careful reading of numerous papers (especially in combination) indicated to us that weather related changes in forage abundance and quality and animal distribution often influenced large mammal population dynamics regardless of density. Low density populations did not perform well during unfavorable conditions, but high density populations could perform well during favorable conditions. This seemed to be true across a wide variety of species and locations: wildebeest in Masailand (Talbot and Talbot 1963) and Kenya (Croze et al. 1981), white-tailed deer in Texas (Teer et al. 1965), blesbok in South Africa (du Plessis 1972), African buffalo in the Serengeti (Sinclair 1977), black bear in Minnesota (Rogers 1987), mountain sheep in California (Wehausen et al., 1987), and mule deer in Montana.

Talbot and Talbot (1963) reported that drought was the primary factor controlling reproduction of wildebeest in western Masailand. They stated (p.71):

> "Low nutrition plane in wildebeests appears to be caused by lack of green forage. Wildebeests in western Masailand, being free to migrate widely following rains, showed no evidence of low nutrition. Wildebeests on the Athi-Kapiti plains, however, being restricted throughout the year to their former wet-season range, show evidence of low

nutrition affecting reproduction even under relatively mild conditions."

Similarly, Teer et al. (1965:56) stated: "Changes in carrying capacity occur rapidly and frequently, and are often independent of density of grazing herbivores." Du Plessis (1972) noted that "Blesbok lose condition during the dry season." Rogers (1987) reported that reproduction in black bears was controlled mainly in a density-independent manner by fruit and mast supplies that fluctuate in abundance from year to year.

Although the influence of various factors on population dynamics sometimes varied with density, density was not a consistently regulating factor nor did it function deterministically. Often, density was only a coincident factor, thus regression analyses and correlations can result in false conclusions about cause and effect. Population growth and decline were both limited by the length of time that extrinsic factors (especially weather) remained either favorable or unfavorable. This, together with the behavioral and biological capabilities of the animals, determined the "distribution and abundance" of the deer.

It is clear that application of regulation or limitation theory must take variable exogenous factors into account. These factors, for many populations, tend to hold them below densities where density-dependent processes might operate. To date, with rare exceptions, too little emphasis has been placed on variable environmental conditions and heterogenous habitat. The natural tendency of man is to lump, type, or categorize, thus variability has been considered the exception. We maintain that variability and heterogeneity are more pervasive and applicable than stable equilibria.

The importance to population dynamics of heterogeneity of the environment in both space and time interacting with characteristics of the animal species will perhaps be more clearly portrayed by use of illustrations. Heterogeneity of habitat quality and quantity in space is illustrated by Figure 12.1. The relative mix and juxtaposition of types of habitat quality and quantity will vary from area to area, by species, and by ecological amplitude of the species. Despite and because of this variability, the major point of Figure 12.1 remains; habitat is heterogeneous in space, not all space is equal in habitat quality and quantity. The performance and fates of individual animals occupying individual home ranges will vary as individuals, not as 1/N.

Habitat quality and quantity are also heterogeneous in time (Fig. 12.2). Habitat quality and quantity in the 3 different time periods illustrated (Fig. 12.2 A, B, and C) do

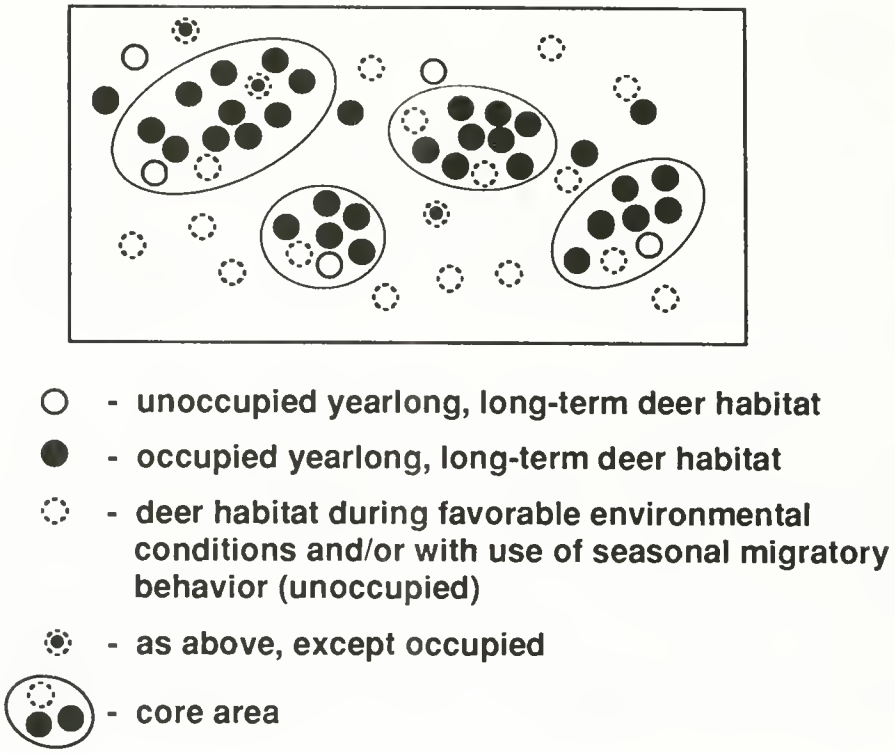

○ - unoccupied yearlong, long-term deer habitat
● - occupied yearlong, long-term deer habitat
- deer habitat during favorable environmental conditions and/or with use of seasonal migratory behavior (unoccupied)
- as above, except occupied
- core area

Figure 12.1. A schematic representation of the variability in space of habitat quality and quantity.

not necessarily follow consecutively. Any of the scenarios illustrated could follow any other. Variable weather can result in rapid changes in habitat quality and quantity from year to year and season to season. Variability in weather not only results in rapid changes in forage quality and quantity (Chapter 3) and thereby fawn survival (Chapter 5), but also by interacting with the fixed habitat base, it influences whether space is reproductive, survival, or non-habitat (Chapters 3, 5-10). Thus, habitat quality and quantity are variable in time, especially as influenced by the inherent variability of the weather, but also as influenced by succession, fire, and many of man's activities.

This heterogeneity of habitat in space and time interacts with the inherent characteristics of dispersion and dispersal for any animal species to further influence population dynamics. A hypothetical species distribution at a population low is illustrated in Figure 12.3A. This distribution and population low could have resulted from a variety of causes (e.g., drought, severe winters, or overharvests). Given favorable environmental conditions and/or low harvest rates, the distribution of the species can progressively expand toward "habitat fill" as illustrated by Figure 12.3B and C.

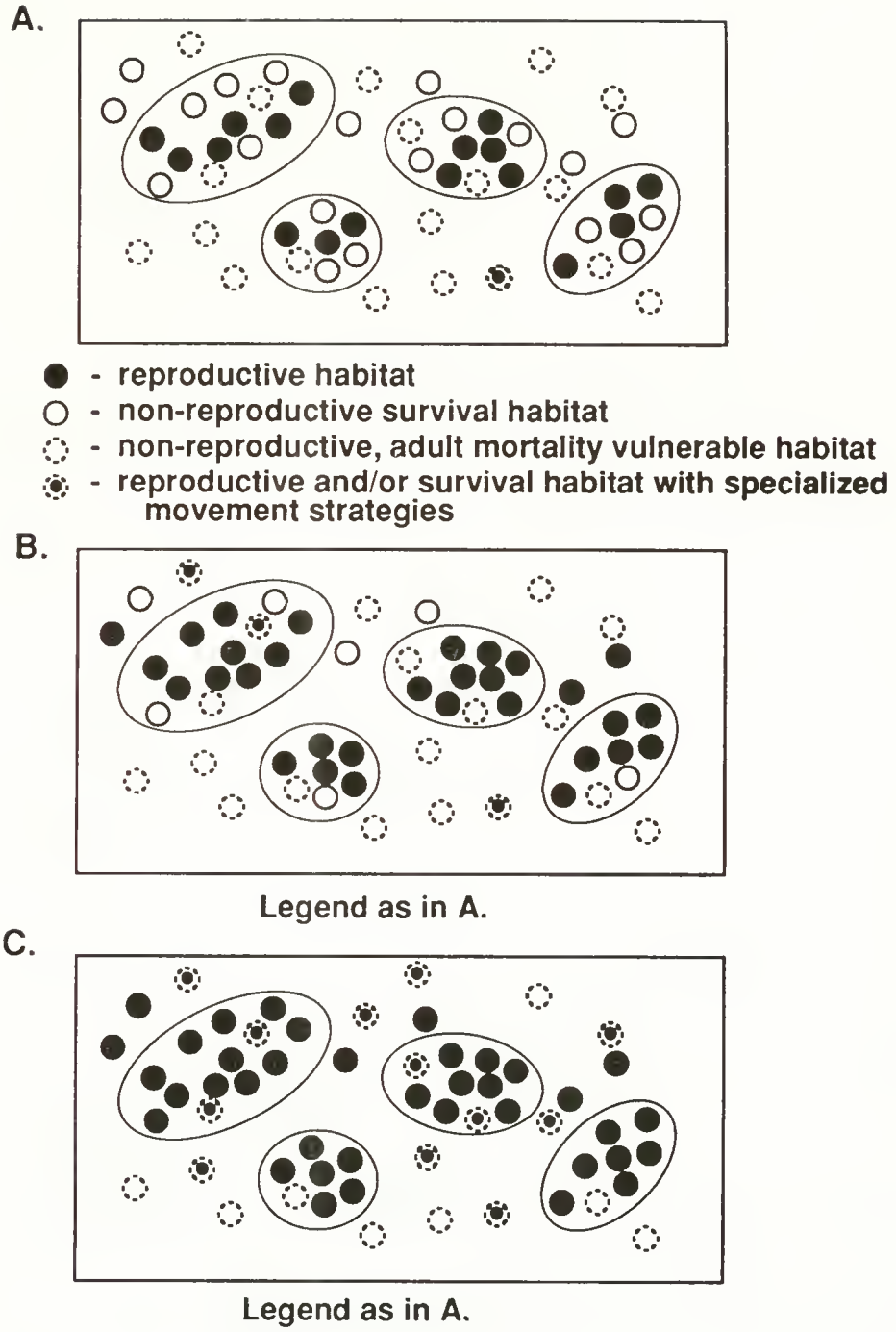

A.
● - reproductive habitat
○ - non-reproductive survival habitat
◌ - non-reproductive, adult mortality vulnerable habitat
⊛ - reproductive and/or survival habitat with specialized movement strategies
B.
Legend as in A.
C.
Legend as in A.

Figure 12.2. A schematic representation of the variability in time of habitat quality and quantity. Figures A, B, and C represent independently different time periods, they are not necessarily consecutive periods.

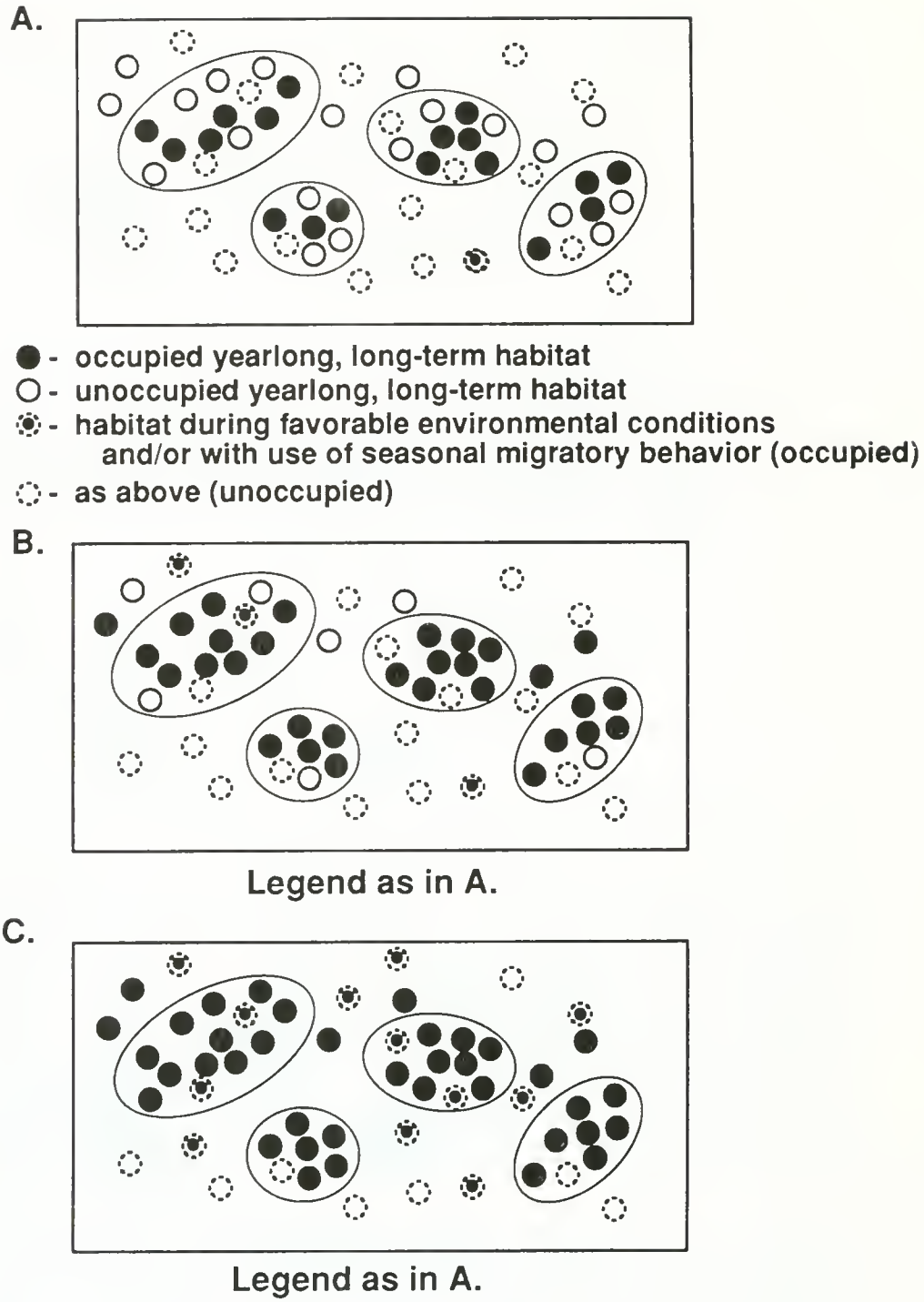

A.
● - occupied yearlong, long-term habitat
○ - unoccupied yearlong, long-term habitat
- habitat during favorable environmental conditions and/or with use of seasonal migratory behavior (occupied)
- as above (unoccupied)
B.
Legend as in A.
C.
Legend as in A.

Figure 12.3. A schematic representation of habitat fill over time given favorable environmental conditions. The progressive filling of habitat by dispersion and dispersal is represented in consecutive order from a population low (A) through mid-fill (B) to near habitat fill (C).

The species social structure and behavior (Geist 1971) along with its reproductive potential and morphological, physiological, and genetic characteristics determine its rate of dispersion and dispersal. Thus, given favorable environmental conditions, distribution of microtine rodents might progress from A to C and beyond (Fig. 12.3) in a year or less. For deer (*Odocoileus* spp.) and moose (*Alces* spp.), 4 to 5 years might be necessary for expansion of their distribution from that represented by Figure 12.3A to that in Figure 12.3C. An equivalent expansion in distribution might take decades for species such as mountain sheep (*Ovis* spp.) (Geist 1971).

Clearly then, the species rate of dispersion and dispersal is another time factor important in population dynamics, particularly in variable environments. Species with rapid rates of dispersion have the potential to reach "habitat fill" (Fig. 12.3C and beyond) during periods when environmental conditions remain favorable. These species are more likely to at least occasionally reach "habitat fill" and perhaps display "density-dependent" dynamics. Species with relatively slower rates of dispersion may seldom display density-dependent dynamics because environmental conditions suddenly may become unfavorable before sufficient time has passed for them to reach "habitat fill".

The relative stability of different environments is also an important consideration in determining population dynamics. Thus, relatively stable environments are more likely to provide adequate time for "habitat fill" to be achieved while more variable environments provide less time under favorable conditions for "habitat fill" to occur. This combination of factors leads us to the hypothesis that species with rapid rates of dispersion that live in stable environments are more likely (though not guaranteed) to reach densities where a significant degree of "density-dependent population dynamics might be observed than species with slower rates of dispersal that live in variable environments.

A counter to the foregoing argument might be that species with slower rates of dispersion and dispersal are more likely to increase within place, placing increased pressure on local resources. Thus, these slower dispersing species might be most likely to exhibit density-dependent dynamics. This argument certainly needs more consideration and investigation. Tentatively, however, our observation is that slower dispersing species are usually those which also have lower reproductive output. Thus, environmental conditions usually turn unfavorable before local densities have the opportunity to reach extreme levels. Also, species populations that live in variable environments tend to have rapid, not slow rates of dispersal. Dispersal rate may also vary within a species, depending on the environment in which they live.

An alternative way of viewing population dynamics in variable environments is that "carrying capacity" (in whatever manner it is defined) fluctuates widely and unpredictably. Thus, some may assert that although measurements using absolute density may not show predictable density-dependent relationships, population dynamics may respond to relative density. Our data did not show a response to relative density for the Missouri River Breaks mule deer population. Furthermore, if fluctuation in "carrying capacity" is primarily caused by density-independent factors (as we observed), then there is no feedback loop, hence no regulation.

Why was this population limited by "random" or chaotic extrinsic factors rather than density-dependent regulation? Actually, our results are not unusual for free-ranging populations. There has been no substantial evidence presented to "prove" density-dependent regulation for free-ranging "natural" populations (see Chapter 1). The only substantial evidence for density-dependent regulation has come from laboratory, penned, introduced, or island populations and possibly from populations for which predators had been eliminated. Cohen et al. (1980) recognized this when they stated (p.xv):

> "Laboratory studies...tend to present a picture of populations well regulated and largely self-regulated...Because food, predation, and disease [also weather and emigration] are not allowed to act as limiting factors, exogenous controls appear unimportant, and since random environmental events are prevented from impinging, equilibrium states are readily observed."

They further stated (p.x):

> "In fact, an informed consensus of the participants in the symposium, pre-selected in large part for their interest in internal regulation, was that there is enormous variation both among species and among habitats in the relative importance of self-regulation; that...mechanisms of self-regulation are at some level probably fairly common among animal species; but that for most species they may only rarely come into play in periods when exogenous forces do not first intervene."

Similarly, Botkin et al. (1981:373) state:

> "One of the problems with much existing population theory for large mammals is its failure to view the animals within an ecosystem context. Standard

> approaches...logistic, Lotka-Volterra, Leslie Matrix are deterministic and abstract, ... populations are treated independently of most of the variability of the environment and biographical forces."

Thus, although various studies provided evidence for density-dependent regulation under precisely specified and often unrealistic conditions, management application of the principles derived has often proven inappropriate or even disastrous for free-ranging populations. Wildlife managers have actually paid too much attention to population theorists.

Similarly, impressions left by early writers, when left unchallenged for decades, became unconsciously assumed "law". For example, one of the major themes of the writings of Malthus and Darwin is that of the tremendous reproductive potential of species. We have been unconsciously left with the impression that populations are always straining against "carrying capacity". This often unrecognized assumption has been inherent in much of population theory despite the fact that "carrying capacity" was not defined or measured. When "carrying capacity" was defined or measured, it often turned out that populations were not at or near "carrying capacity". Just awareness of the possibility that populations are not always pressing against "carrying capacity" or "trying" to exceed it can lead us to new ways of thinking about population regulation and especially management.

We believe we have shown that a multitude of factors can and do affect population dynamics. The relative impact of these factors can vary among species and among species populations inhabiting different environments. For the mule deer population inhabiting the widely fluctuating environment we studied, important limiting factors included: the length of time green forage was available, the energy demand by deer, predation, emigration rate, and hunter harvest. All these factors were influenced or controlled to some degree by weather, the first 3 especially so. All <u>limiting</u> factors interacted such that the opportunity to observe density-dependent <u>regulation</u> did not occur.

It is possible that conditions leading to density-dependent regulation could occur, given changes in the environment. For example, limitation of emigration by fencing or lack of dispersal sinks, annihilation of predators, and/or cessation of hunting singly or in combination could result in density-related resource shortages leading to poor condition. Thus, population dynamics could be altered toward density-dependent regulation. We believe, however, that many, if not most, free-ranging "natural" large mammal populations are usually <u>limited</u> by variable extrinsic factors below densities

where potential density-dependent regulation might be observed.

The conclusions we have reached about the lack of a neat and tidy "balance of nature" or "regulating mechanisms" may be unsettling to some. There is, however, no reason for panic; "chaos" is not as intimidating as it first seems. It is, perhaps, a desire of most of us that there be order, measurability, and predictability in our world. This desire may have even affected Albert Einstein's lack of acceptance of the uncertainty inherent in the quantum theory that eventually evolved. This view reportedly led him to state emphatically to Niels Bohr that "God does not play dice [with the universe]" (Calder 1979). More recently, Joseph Ford, a physicist at the Georgia Institute of Technology, has answered Einstein (quoted by Gleick 1988 p.314): "God plays dice with the universe. But they're loaded dice. And the main objective of physics [or ecology] now is to find out by what rules were they loaded and how can we use them for our own ends."

Explanations for the behavior of weather, a major factor influencing population dynamics, have come more and more to rely on "chaos" theory (Gleick 1988). What at first appears to be chaos, is upon further examination, channelized randomness or ordered disorder (Gleick 1988). This "channel" of variation (or loading of the dice) is measurable and environmental variation and population level and dynamics will remain within the bounds of that "channel".

The lack of evidence for deterministic and consistent self-regulation or other forms of density-dependent regulation of many populations need not be controversial or disquieting. Before, during, and continuing after the times we have argued about mechanisms and theories of regulation, populations have generally varied within natural channels. We have not found the "balance of nature" we sought because we looked in the wrong places. A "balance" does occur--it is in the environment. There, over time, unfavorable conditions are balanced by favorable conditions. Rarely, natural catastrophes may perturb a population outside its "natural" channel. In that case, another natural phenomenon may take place--local or large scale extinction.

More frequently of late, it seems, man's activities may perturb environmental conditions beyond the natural channel of animal adaptability. Extinctions that may result in these cases are preventable and thus, are cause for concern. Reliable information on natural environmental variability and animal adaptability and fixed habitat requirements will be necessary to address the impacts of human activities.

CHAPTER 13

MANAGEMENT IMPLICATIONS

Management Philosophy and Theory

As indicated in Chapter 1, most population and habitat management for ungulates has been based on the belief that density-dependent regulatory processes are in fact operating on/within the population and that they apply at all population levels (are logistic). It is most commonly assumed that intraspecific density-dependent competition for resources (especially food) defines "carrying capacity" (K). In most models, K is displayed as relatively stable and influenced primarily by the animals through grazing and browsing pressure. Generally, because of their reproductive potential, populations are portrayed as always straining to exceed "carrying capacity" (inherently irruptive).

Some of the more common concepts or "principles" derived from density-dependent theory and applied in deer management include: compensatory reproduction, compensatory mortality, maximum sustained yield, intraspecific competition for food, winter "bottleneck", "doomed" surplus (insignificance of predation), finite "carrying capacity", the "law of diminishing returns", and various approaches to habitat management. Many of these concepts, "principles", or "laws" have come to have a life of their own, without recognition of the assumptions behind them.

For mule deer in the Missouri River Breaks (MRBMD), density-dependent processes were not consistent, precise, or predeterministic (if they occurred at all). Variable effects of limiting factors led to both low recruitment/high mortality and further population declines at low densities and high recruitment/low mortality and further increases at high densities. "Carrying capacity" was not easily or simply definable whatever criteria were used. Forage production and quality as well as usable space fluctuated independently of density. Population growth rate declined to zero or below at low as well as high densities. It also was explosive at both relatively high and low densities. Expected compensation in reproduction and mortality was not observed. Gradually, it became obvious that management concepts based on density-dependent population regulation seldom applied.

Our discussion of management implications and recommendations centers on mule deer in fluctuating environments that include predators and dispersal sinks. We suspect that many of our findings and concepts will apply in some degree to other areas, and perhaps to other species in similar environments. However, we caution the reader against

a common problem in converting science to management; the overapplication of findings from one area or species to others.

Management Concepts

The implications of our findings to management are dissimilar to those usually encountered. Therefore, we believe it is necessary to first discuss some common management concepts in relation to our findings before making recommendations.

Management of ungulates has usually centered around the concept of a forage based "carrying capacity" (K). Because much of the observable natural mortality occurred during winter, it has further been assumed that there was a winter "bottleneck" and that the quantity and quality of winter forage was a key factor determining "carrying capacity". Thus, "carrying capacity" and population dynamics in deer have most commonly been interpreted to directly relate to the quantity and utilization of winter forage, especially "key" browse plants.

Additionally, deer populations have been assumed to be inherently irruptive, which led to "over-utilization" of forage and a reduction in "carrying capacity". Management strategies emphasized the importance of hunter harvests to bring deer numbers into "balance" or "equilibrium" with forage supplies (especially winter forage) and prevent overuse of browse plants. Similarly, it has been believed that populations held somewhat below "forage carrying capacity" were the most productive and would yield maximum sustained harvests. A reduction of the number of deer on "over-used" range would reduce browsing pressure and result in improved forage condition and production, thereby improving fawn production and survival for the remaining deer. Thus, hunter harvests were deemed to be compensated for by increased reproduction (compensatory reproduction) and decreased mortality (compensatory mortality) among survivors. Because deer were considered to be inherently irruptive, both hunter harvests and kills by predators were considered to substitute for (not add to) mortality of the "doomed surplus" from starvation or other causes.

For our study area and mule deer population, forage production and condition were primarily determined by factors other than deer browsing pressure (Chapters 3 and 10). Forage production and quality were determined mainly by variation of temperature and precipitation. Deer browsing pressure did not result in long-term deterioration of forage plants and in many cases actually stimulated increased production of browse plants (Mackie 1973b, Peek et al. 1978). Measures of "forage

carrying capacity" varied many-fold among years independently of deer density; forage quantity was not limiting during any year or season. Variation in forage quality (nutritional content) among years and the length of time nutritionally adequate forage was available in any year was of major importance to mule deer population dynamics. Because quality of winter forage was typically only of maintenance or lower quality, we determined that forage conditions during spring through autumn were of vital importance. The overall physical condition of deer and amount of fat that they carried into winter comprised a major component of "winter range". Length and severity of winter were important as they influenced the rate of use of fat reserves and the length of time deer were forced to subsist on maintenance or sub-maintenance quality forage.

Although the length of time that high quality forage was available had major influence on population dynamics, there was no evidence that intraspecific competition for food played a major role in determining nutritional plane of deer. Thus, management concepts tied to intraspecific density-dependent competition for food, finite carrying capacity, and "winter bottlenecks" had little applicability to this population. As evidenced by the combination of a variety of literature cited throughout this report (Chapters 1, 3, 5, 10-12), similar conclusions may also be drawn for some other areas and populations.

Because intraspecific competition for food was not a major influence on population dynamics, the concepts of compensatory reproduction and mortality also are questionable, at least for this population. We were, in fact, unable to measure significant compensation. When nutritional deficiencies are primarily independent of the number of deer on the area (density), reductions in the number of deer do not improve nutritional conditions. It follows that, if nutritional conditions are not improved, reproduction and survival do not improve and there is little or no "compensatory" (increased) reproduction or "compensatory" (decreased) mortality among surviving deer.

An additional and separate aspect of the issue of compensation is the question of whether hunting mortality substitutes for or is additive to other forms of mortality. This is the "compensation" typically referred to across all wildlife species. For example, game birds are rarely, if ever, considered to destroy their food base, yet most of their mortality by hunting is considered "compensatory mortality" in the sense that it generally substitutes for other mortality. To keep this form of compensation separated (as it should be) from that addressed in the previous paragraph, we will use the term substitution. Thus, we frame the question: does hunting

mortality substitute for or add to natural mortality? Also, does mortality from coyote predation substitute for emigration or mortality from starvation and "old age"?

Obviously, at least some hunting mortality substitutes for natural mortality that would occur in any case; the question is how much? Our data indicated that this varies among sex and age classes and probably among locations and species. Because forage conditions for survivors were not improved as the result of death of individuals, substitution probably only functioned on an exact basis. That is, if the specific animal harvested was one that was "doomed" to die overwinter, then that hunting mortality substituted for natural mortality and was not additive to other mortality. On the other hand, the harvest of a healthy, fat 3-year-old female could not and did not prevent a malnourished fawn (or 16-year-old female) from dying. Similarly, the harvest of deer in core habitat did not guarantee survival of deer in marginal habitat. Thus, the degree of substitution depends upon the varying annual percentage of the population vulnerable to "natural" mortality.

The impact of additive hunting mortality to the population depended upon subsequent recruitment rates that determined replacement. Thus, even though a varying degree of hunting mortality was additive to other mortality, population declines did not occur when recruitment was adequate to replace that mortality. Because recruitment rates varied substantially among years, the effect of any given rate of hunting mortality also varied among years.

Pre-season male:female ratios on our study area were not much different in many years than those reported for unhunted populations. Thus, much hunting mortality of adult males appeared to substitute for high natural mortality which would probably occur in the absence of hunting. Our data suggest that the degree to which pre-season male:female ratios are below about 40:100 may indicate the extent to which hunting mortality of males is additive to natural mortality.

Hunting mortality of adult females did not substitute for natural mortality to the same extent as for males because of lower natural mortality among females than males. Also, the removal of adult females by hunting potentially affected future population dynamics more than removal of males because it more directly affected future numbers of fawns produced. Because emigration by yearling females probably increased at high densities, there is likely an increased degree of substitution for hunting mortality of adult females by yearlings remaining in or returning to the population.

Because of their higher natural mortality rate, a greater percentage of the hunting mortality of fawns substituted for natural mortality than occurred with adult females. However, the low hunting mortality rate of fawns resulted in little realized substitution on a population basis.

As a result of the above, the degree of substitution of hunting mortality for natural mortality (compensation) in the Breaks population probably varied quite widely. Substitution may be greater at high densities or when natural mortality rates are high. There may be almost no substitution when deer numbers are low or deer are in excellent condition. The degree of substitution also varies among sex and age classes and among individuals within those classes. Again, when analyzing all population processes, it is important to recognize that deer are individuals (not 1/N).

The impact of predators on the population can be viewed similar to that of hunter harvest, although there are some differences. Like hunting, the extent to which a predator kill substitutes for other mortality will often also depend upon the exact animal killed. In the Missouri River Breaks, coyotes killed much higher proportions of fawns than did hunters. Similarly, coyotes killed higher proportions of older animals that were wounded, sick, or otherwise predisposed to mortality. Thus, a higher proportion of the deer killed by coyotes than by hunters substituted for losses that would have resulted from malnutrition, old age, or emigration.

Not all mortality of deer by coyote predation substituted for other mortality, however. Results of this and other studies indicated that coyotes can and at times do kill significant numbers of healthy deer that would have survived in the absence of predation. The concept that predators kill only the "doomed surplus" and do not cause population declines is based on the erroneous assumption that reproduction always produces more animals than the habitat will support. Clearly, mule deer populations in the Missouri River Breaks were not always near habitat fill, and predators did kill animals that were not "doomed surplus". Similar to the effects of hunter harvests, predation by coyotes appeared to have its greatest impact when deer densities were low. This probably occurred because there is little opportunity for substitution at low densities (few vulnerable, old, etc.) nor can good nutritional conditions and good fawn recruitment be guaranteed.

Why do our conclusions differ from traditional views about the occurrence and application of compensatory reproduction and mortality? The "principles" of compensation have generally been based, and especially applied, on the assumption that nutritional deficiencies resulting in poor

reproduction and survival were always dependent upon density of the study population. Our findings plus those becoming increasingly common in the literature indicate that nutritional deficiencies are not always, or even often, related to density in free-ranging populations.

Many people (especially lay persons) have recognized that substitution probably doesn't occur on a 1:1 basis. Early management programs, however, in practice appeared to assume 100% substitution and guaranteed compensatory reproduction and mortality at all densities and times. There was no database to challenge those assumptions until hunting mortality rates began to rise above natural mortality rates.

Differences in interpretations about the importance of compensation and substitution are also rooted in the inherent characteristics of the species studied. In hindsight, it is easy to understand some conclusions resulting from early studies of insects, fish, and birds, all of which had high annual or generational rates of natural mortality. Only recently have long-term data become available for larger, longer-lived species with relatively low rates of natural mortality.

For a game bird population with an annual mortality rate of 50-80% in the absence of hunting and for which young of the year are not selected against by hunters, a high proportion of hunting mortality might be expected to substitute for other mortality. Should the same degree of substitution be expected for adult female mule deer in the Missouri River Breaks with an average annual natural mortality rate of 7-8%? Obviously not. Thus, the conclusions of early studies were safe until relatively recent times, when hunting mortality began to exceed natural mortality rates by a significant degree in more and more places.

The higher degree of substitution (compensation) likely for game bird populations does not mean that additive effects of hunting mortality can be ignored for these species. First, game birds as well as deer must be considered as individuals. Chances of natural mortality vary at least somewhat by sex and age class as well as place of residence. Thus, even for a species with an annual natural mortality rate of 70%, substitution isn't 100% efficient all the way up to 70% hunter mortality. At least some fraction is additive. Second, similar to what occurred with big game populations (and similarly still unrecognized), harvest rates may be creeping up to and exceeding the natural mortality rate in some locations. If an "unexplained' crash occurs in some local areas in the future, it may not all be explainable by loss of habitat or bad weather.

The concept of maximum sustained yield assumes that populations maintained below maximum density are more productive and yield greater sustained harvests than high density populations. We observed 2 major problems with application of this concept in management. First, net recruitment may not be related to population density; for the MRBMD population it certainly couldn't be predicted from density. Thus, yield was not predictable (and sustainable) at any population level. Second, even if density-relationships applied, forage-based "carrying capacity" fluctuated so much that attempts to achieve stable population levels and sustainable yields were impractical. Yields were not sustainable at any population level, but tended to be higher at higher population densities (Chapter 5).

The "law" of diminishing returns also needs further discussion. At times, we have heard this concept confused with compensatory mortality. The statement usually goes something like this: "There is compensatory mortality because if deer become too scarce in one area, hunters compensate by moving to another area, thereby lowering mortality in the former area." The concept of diminishing returns and the extent to which it may be operative need to be updated. Long ago, Aldo Leopold (1933) recognized that the level of operation of "diminishing returns" and hunter effectiveness are variable when he stated: "gasoline has not lengthened the tether of the bobwhite". Habitat security is much more than vegetation composition, interspersion, and topography. Changes in access, hunter affluence, mobility, leisure time, equipment, and desire can alter habitat security as surely as changes in vegetation composition. What was "secure" habitat yesterday may be insecure today even without environmental change. Reliance on the "law of diminishing returns" to affect changes in hunter distribution and hunting pressure can result in hunter dissatisfaction (Wood et al. 1989). Use of the "law of diminishing returns" as a management tool will result in unhappy customers and would not be employed in competitive businesses.

Finally, we address concepts of habitat management. Because of the overriding influence of the concept of a forage-based carrying capacity, most habitat management for ungulates has focused on practices that "improve" forage conditions, particularly on winter range. Indeed, the philosophy of reducing deer populations to at least somewhat below "carrying capacity" has been considered habitat management because it is intended to improve forage production and the condition of forage plants. The U.S. Forest Service often justifies timber cutting on the basis that it improves forage production for ungulates. Many State Game Departments buy land (especially winter range) for the purpose of preserving and enhancing forage for ungulates. Although

forage is an important consideration in habitat management, the ways in which it is important include more than simply quantity, and other aspects of habitat may be of equal importance in management. For example, more recently, with the advent of heavier hunting pressure, the importance of cover has also received increased recognition.

General Approach to Management

The general approach to deer management we recommend remains very similar to that outlined in earlier Montana Deer Studies reports (Mackie et al. 1980, 1985). Here, we discuss the conceptual basis for a general approach to deer management. Findings of this study together with those of other Montana deer studies indicate that each deer population is a unique product of its total environment. The range of characteristics and responses for each important population can be established, indicating the range of potential management options. Our model of population-habitat relationships and dynamics (Fig. 1.4) indicates that the level and variability of resource outputs interacting with animal strategy determines population dynamics. Thus, the first step of management is to gather data on characteristics and variability of both the deer population and the environment. Though both types of data are desirable, one can often be inferred from the other. Population characteristics that should be measured include: population size, sex and age composition, harvest size and composition, seasonal distribution, and mortality patterns. Habitat variables to be similarly quantified include: seasonal and annual temperature and precipitation, snowfall, winter severity, and plant phenology, especially timing and length of the "green" period. In most cases, these data will be available for 10 years or more; if not, collection should begin immediately. Most of the necessary environmental data will usually be available for correlating environmental events and characteristics with population responses. Such correlation will result in some degree of predictability for population responses. Management strategies can be based on expected population behavior and thus, <u>if desirable</u>, can be specific to individual populations.

Population Evaluation and Management

Harvest Management

Harvest strategies and management will vary among individual managers, with the desires of local hunters, landowners, and outfitters, and with local environmental characteristics. Thus, management depends as much upon psychological, sociological, and economic considerations as upon ecological considerations. For instance, some managers and hunters prefer consistency of hunting regulations across

areas and from year-to-year, despite the resulting increased fluctuation of populations. Others may accept variable regulations if they result in moderated population fluctuation which make expectations for hunting success more consistent.

Although psychological, sociological, and economic aspects of management cannot be ignored, our main purpose is to assure that the biological and ecological background to management is sound. Thus, management decisions will have at least considered realistic biological potentials, and probable population responses of management actions will not be unanticipated.

In variable environments like our study area, a harvesting strategy based on average recruitment and mortality rates or the role of compensatory reproduction and mortality will seldom track population trend. During extended periods of below-average recruitment and above-average natural mortality, the population will decline under an "average" harvesting strategy. On the other hand, during extended periods of above-average recruitment and below-average natural mortality, the population will increase. If sufficient dispersal to vacant habitat has occurred and the goal is to stabilize populations, above-average harvest rates must be implemented during increasing phases.

In variable environments, the use of an "average" harvesting strategy increases the fluctuations of a population, rather than dampening those fluctuations. A "tracking" harvest strategy (Caughley 1977), with specific numbers of tags valid for antlerless deer would more closely respond to population trend. This concept and other discussion of harvest strategy were discussed in more detail in Chapter 6 - Adult Mortality. If managers prefer consistence of regulations from year to year or across environmental types, they must be prepared to accept the implications of populations occasionally declining below the normal low. Social, economic, and political factors will often dictate "crisis" management measures when deer populations fluctuate to "unacceptable" levels.

Harvesting deer in variable environments is not a simple scientific or mathematical exercise of calculating stable averages, yield curves, and tag numbers using computer models. Extrinsic factors, including hunting mortality, do not act in an average manner and there are no average deer. Natural mortality rates are different for different sex and age classes and among areas and years. Fawns have higher mortality rates than adult females. A female that has recruited fawns for 2 or more years in a row is more likely to die over-winter than one that lost her fawn in June and recovered body condition during summer and autumn. An older,

dominant breeding male is likely to be in poorer condition entering winter than a yearling male. All males usually enter winter in poorer condition than females. Adult males are harvested at a higher rate than yearling males and all antlerless deer, adult females are harvested at higher rates than fawns, and different age classes of adult females are harvested disproportionately.

Because adult females have a lower natural winter mortality rate than fawns, the potential level of compensatory mortality between age classes is further reduced. Although fawns have a higher natural mortality rate than adult females, most of their annual mortality takes place between birth and the hunting season. Thus, hunting mortality can only potentially substitute for the fraction of fawn mortality that occurs over winter. Hunting tags valid only for fawns could potentially increase the operative level of compensatory mortality (substitution) in populations. The actual level would, of course, vary among populations and years, but would be somewhat higher if more fawns were harvested.

Deer were not harvested equally across our study area even though there was reasonably good access to all parts of the area. Deer in more marginal, open habitat, close to roads, and on ridge tops were harvested more heavily than those whose home ranges were in rugged, diverse core areas. This also, at least partially, explains why hunters on this area don't perceive many deer until the marginal habitat begins to be filled. That typically occurred when the area-wide density exceeded about 3.9 deer/km^2. Thus, maintenance of deer in marginal habitat was important to maintaining hunter satisfaction, but it reduced the degree of "substitution" that could occur.

All of these variations among sex and age classes, among individual deer, and in hunter response to them, when combined with the unpredictability and annual variation in weather patterns and predation levels, made yield models impractical. Instead, improvements in harvest efficiency can be made only by directing kill to certain sex and age classes and to certain areas or habitats. Changes in harvest strategies must be made quickly and as near the opening of the season as possible to be most efficient. If such changes are impractical or if we desire consistency and continuity of regulations, then we must resign ourselves to either a greater degree of fluctuation in deer populations or more conservative hunting seasons than might otherwise be possible.

Because generalized density-dependent compensatory mortality and reproduction did not operate effectively in the MRBMD population, we must not allow ourselves to be deceived by the implied precision of existing models that incorporate

such processes. Harvesting strategies that are currently practical do not even closely mimic the culling and "harvesting" practices of domestic livestock operations which make use of "substitution".

Normally, domestic cattle ranchers attempt to cull and sell older, unproductive, and unthrifty cows before they die. Similarly, "cow-calf" operators sell the major portion of the crop of young-of-the-year shortly after weaning, retaining the best calves to replace adults that were culled. Although not 100% efficient, generally those animals most likely to die or decline in productivity are sold for a return rather than retaining them in the population.

If on 1 October each year, the rancher randomly, rather than selectively, removed 20-30% of his cows and calves for sale, some additional mortality would almost certainly occur during the next year among vulnerable animals not selectively culled. In this case, the rancher employed a harvesting strategy similar to most "enlightened" wildlife harvesting strategies that harvest a portion of the females and young. The point of this example is that even for areas or species in which some density-dependent compensatory mortality and reproduction are considered to be a valid component of models, we should not assume anywhere close to 100% efficiency of operation. At least some harvesting loss will always be additive to other losses. Recruitment must match harvests <u>plus</u> additional natural loss to maintain stable populations.

Where habitats contain interspersed public and private lands, the distribution of harvest in both space and time has important implications to population dynamics. Hunters seem to prefer to not ask permission to hunt on private land if public land is available. Part of the mystique of hunting is the sense of freedom and "providing for yourself". In Montana at least, asking permission violates both desired products. At some point, however, overcrowding on public land reduces the sense of freedom and the deer population enough to increase the attractiveness of hunting on private land. This situation aids those interested in "privatization" of wildlife and argues against overharvests of deer on public lands. It may also indicate that high sustained harvests and maximum opportunity for everyone is not a unanimous public goal for management on public lands.

Because of the above and other considerations, uncontrolled distribution of hunting pressure often results in overharvests of "roadside" deer and deer on public lands. Thus, core populations in secure habitat and populations on private lands with limited access can remain relatively unchanged while hunter dissatisfaction generally increases.

Self-distribution of hunters seldom helps solve game damage problems until extreme levels are reached. Early prevention of game damage is certainly not achieved by free-choice distribution of hunting effort.

Our studies have shown that varied and specialized movement and home range strategies are necessary if habitat fill is to occur in complex, diverse, and variable environments. On our study area, autumn and winter migratory movements were necessary if deer were to successfully occupy shallow relief areas from late spring through autumn. Similarly, mule deer populations in mountainous areas also have migratory segments. Some of these may be long-distance migrants, occupying summer range far from the nearest winter range. Significant numbers of these migratory deer are often necessary to achieve habitat fill and maximize population level on many areas.

Long-distance migratory segments often move to winter range earlier than other deer; thus, it is possible for various regulations and/or non-directed distribution of hunter kill to impact some segments longer than and more than others. This learned migratory behavior, passed from mother to daughter, may take some time to re-establish if excessive harvests remove significant numbers of these long-distance migrants. This problem may be especially important in mountain deer populations where low recruitment rates prevail. It is possible that very heavy harvests of antlerless deer from some western Montana populations in the late 1950s and early 1960s almost entirely removed early migratory segments with traditions of long-distance migration. Thus, some summer range at long distances from winter range remains unfilled, and total population size has never recovered.

For riverbreaks and prairie populations that move to "winter range" only during very severe winters, excessive antlerless harvest during the intervening years may result in little "population memory" of wintering areas. Although the remaining deer may eventually find these areas by wandering during subsequent severe winters, additional mortality may result because few deer remain that remember the appropriate immediate response.

In many cases, population managers may determine that changes in regulations affecting distribution of kill in time and/or space are impractical or undesirable. However, they should at least be aware that broadbrush approaches to management can affect subtle changes which may have long-lasting impacts on the population.

Our findings also had some implications with respect to the current concern of some segments of the public for

managing for larger and/or trophy males. Our data, like findings of many other studies, indicated that males and females used habitat differently, and to some extent used different areas. This partitioning of habitat and location appeared to have its basis in parturition territoriality of females. It suggested a hypothesis that potential male:female ratios were at least partially determined by the relative proportions of reproductive and non-reproductive habitat within an area. The difference between potential ratios and actual ratios were primarily determined by hunter harvests and recruitment rates. Some population-habitat units, composed primarily of reproductive habitat, may not have the potential to support high numbers of males. In such areas, "trophy" management would likely be unsuccessful. Habitat security will also affect the potential of an area for "trophy" management. Areas with low habitat security will not produce older males with even moderate hunting pressure.

The extensive emigration and immigration by yearling males on our study area indicated that attempts to "carry over" males within a single, small hunting unit may be unsuccessful beyond certain limits. The level of carry-over will vary with population and habitat, but beyond that the "saved" males may disperse to adjacent hunting units.

In addition to age of the animal, antler size was clearly influenced by forage conditions. Drought and low quality forage resulted in smaller antlers for all age classes. Thus, results of "trophy" management in variable environments will be variable. During some years, antlers will be relatively smaller even when older males are present.

Male:female ratios could be increased in populations which historically had higher ratios than currently observed. For this to occur, however, substantially fewer males must be shot than now occurs. Whether this is accomplished by limited permits or other means, relatively few hunters can harvest males if significant numbers of older males are to be maintained. Even when "trophy" management is implemented, there is no guarantee of improvement beyond a certain point. Dispersal and varying nutritional conditions will also play important roles in reducing the degree of success of "trophy" management. A clear portrayal of what is lost versus what is gained should be made for all potential management actions in each population/habitat unit.

Finally, our data provide for comment about aspects of harvest strategy relevant to game damage problems. Many short-term solutions have been applied toward game depredation problems including various types of fencing, repellents, scareguns, and damage hunts. Stack yards for hay and certain types of fencing have been used for longer-term solutions, but

the most common solution is to attempt reduction of populations through harvest, preferably during the regular hunting seasons. Many types of damage, such as to seed alfalfa or pasture, are more dispersed and do not lend themselves to solutions such as fencing or repellents.

It has become increasingly recognized that many damage problems are chronic and are not necessarily related to population level. In many cases, drought draws deer or other wildlife into the few remaining areas of green forage or to haystacks. This occurs regardless of population level and may involve only a few animals that cause significant damage or the perception of damage. Generalized reductions in deer populations across broad areas do not necessarily stop damage. For some situations where large numbers of deer are not causing the problem, selective local killing by Department personnel of the few deer causing the problem may be the most effective solution.

We should also recognize that in areas of variable environment, many agricultural areas contain the best natural habitat and the best, most dependable sources of high quality forage. Depredation problems in those areas will be chronic. For more than 50 years, we have been encouraging modes of operation and improved land management practices by agriculturists that benefit wildlife. In many cases, improvement has been substantial and deer and other wildlife have benefitted even when increasing wildlife population was not a goal or even desirable to the landowner-manager. Thus, we must recognize that many depredation problems will be chronic and will not be solved by generalized population reductions. Instead, efforts must concentrate on long-term solutions such as permanent stackyards, properly designed fences, and where hunting is allowed, possibly some level of monetary reimbursement or purposeful habitat alterations to reduce deer occurrence.

Predicting Fawn Survival

Advance knowledge of recruitment rates could help deer managers more closely match hunting regulations to population trend. For the Missouri River Breaks study area, we developed a regression equation that accurately predicted fawn survival from data collected by the end of May, just prior to birth. Temperature during May and precipitation during July-May (Chapters 3 and 5) predicted fawn survival during 21 of 27 years for which data were available. Although level of fawn survival wasn't accurately predicted during 6 years, trend was accurately predicted. Our success in predicting trend and level of fawn survival indicates that similar potential exists for predicting fawn survival in other areas. Wood et al. (1989) indicated that similar factors influenced fawn survival

for both mule deer and white-tailed deer in a prairie environment.

Predictions of fawn survival on our study area could not be calculated soon enough to help set general hunting season structure in Montana. However, predictions were available in time to help establish B-tag levels. The relationship between temperature, precipitation, and fawn survival, although not a precise mathematical tool available at the ideal time, does represent a significant improvement in management capability for early response to fluctuating population/environmental characteristics.

Existing weather and deer classification data may be sufficient to attempt to establish similar predictive regression models for other areas. Relationships similar to those described by this study and studies of Wood et al. (1989) might be expected for other non-mountainous areas east of the Continental Divide subject to periodic drought. The exact timing of important periods of temperature and precipitation may vary slightly among areas, but should be generally similar. For areas west of the Divide and other mountainous areas, summer-autumn forage conditions are more dependable and drought is less of a problem. For these areas, length and severity of winter may be more important factors determining fawn survival. Although summer-autumn forage may be of consistent quality in these areas, the length of time deer are able to use that forage may vary with the timing of onset and end of winter. Severity of winter would affect rate of fat depletion.

Predator Management

It was clear both from direct and circumstantial evidence gathered during this study that predation by coyotes influenced mule deer population dynamics. Other recent work on predation also has indicated that the impact of predation is more than just "removal of those animals that were going to die anyway" (Bergerud 1971, Keith 1974, Beasom 1974, Bergerud 1978, Stout 1982, and Gasaway et al. 1983).

We found that the degree of predation on deer by coyotes was influenced by vegetation and forage production and quality which influenced deer behavior and also levels of alternate prey populations. Certain types of snow and ice conditions also influenced predation rates. In some years and some circumstances, coyotes killed many deer that would have survived in the absence of predation. Predisposition of deer by poor physical condition was not necessary for significant mortality by predation to occur. Similarly, O'Gara and Harris (1988) found that a sample of deer killed by coyotes and mountain lions (*Felis concolor*) contained more prime-aged deer

and deer in better condition than a sample killed in collisions with vehicles. Thus, predation involved more than simply "weeding out the young, the sick, and the old".

Coyotes are facultative predators that do not depend upon one major prey species; they successfully use a wide variety of food. Because of this, at low deer densities, coyote numbers will not necessarily decline and deer populations may be subject to significant predation, depending upon the availability of alternate prey. Predation, combined with even low-moderate levels of other mortality (e.g. hunting), can be sufficient to further reduce low density deer populations or at least keep them from increasing. A change in circumstances, such as an increase in alternate prey populations, is necessary to release the deer population from the influence of predation and result in an increase in density. From observations such as this, Haber (1977) proposed a multiple "equilibrium" model in which predators can hold a prey population at low densities, but have little impact at high prey densities.

The implications of these findings to deer population management obviously will depend upon local circumstances, population goals, management philosophy, and political, sociological, and economic factors. At high densities of deer, when alternate prey populations are nearing or at highs, and/or when hunter harvests are insufficient to remove the annual recruitment, managers may be unconcerned with predation or even welcome it. However, if a large decline in the deer population has occurred owing to severe weather or hunting, the manager may want to consider the potential for management actions.

As suggested by Gasaway et al. (1983), management options are limited when a large decline in ungulate populations has occurred, predators are present, and the management goal is to increase ungulate populations. We perceive 4 basic options.

1. No action - The manager can wait for a natural change of circumstances that releases predation pressure on deer. These changes may include a large increase in the availability of easily caught alternate prey, a natural decline in predator populations, and/or favorable changes in weather conditions. These changes could occur very slowly. For example, peaks in jackrabbit populations in this area may be 10+ years apart. This no action option may not be considered viable by many hunters, landowners, and/or managers.

2. Limited action - Here, the manager could also reduce or eliminate harvest of deer by man and wait for the same natural changes in circumstances. However, this

alternative by itself may only halt further population decline or allow a very slow increase in the deer population.

3. Active intervention - The manager could attempt to hasten the increase in deer numbers by reducing predator numbers through various control techniques. Several studies (Beasom 1974, Stout 1982) have shown that predator control can significantly increase fawn survival. This option may be vigorously opposed by some segments of the public and enthusiastically supported by others.

4. "Preventative" management - Where significant predator populations are present, the manager can try to ensure that hunter harvests do not reduce deer populations to such low levels that they become significantly affected by predation. For the Missouri River Breaks mule deer population, that low was about 50-60% of observed population highs.

Of the 4 options, "preventative" management may be the ideal, but significant population decline may also result from severe weather or other non-hunting factors uncontrolled by the manager. In such cases, only the other 3 options are available. The choice among those depends upon many circumstances. Where alternate prey populations seem to be cyclic, it is advisable to know where those populations are within cycles. For example, it might not be necessary to initiate a predator control program when alternate prey populations are naturally increasing. On the other hand, if alternate prey populations have recently "crashed", predator control measures may be more effective or important in maintaining prey population stability.

The option of predator control is particularly subject to political, sociological, and economic considerations. Like biology, any or all could support either side of the issue depending upon location and circumstances. Given the probable difficulty of implementing predator control, it is unlikely that it could often be accomplished on a timely basis. Nevertheless, predator control should not be ruled out of the management repertoire if more rapid population increases are desired. Also, the success of attempts to transplant, re-establish, or otherwise increase low density populations of some species may also depend upon local predator control.

Population Evaluation

Population Estimates

Our data (Chapter 2) indicated that reliable estimates of mule deer populations could be made in riverbreaks habitat. Similar findings were reported for other eastern Montana populations (Wood et al. 1989, Watts unpubl., Knapp unpubl., Jackson unpubl.). Use of complete-coverage aerial surveys and Lincoln Indexes with at least 20-25 well-distributed radio-collared deer was an appropriate method. Observability indexes and other results were generally consistent when the same pilot and observer were used. Once the spectrum of survey conditions had been covered, reasonable estimates of the observability of deer on any particular flight could probably be made by an experienced observer even without marked deer. Surveys with the Bell 47 helicopter were less sensitive to variations in weather conditions and ground cover than those with the Piper SuperCub.

Helicopter surveys and multiple fixed-wing surveys may often be too expensive and time consuming for widespread use by management personnel. When that is the case, and where an estimate of recruited population size is the most important information desired, we recommend full-coverage, early spring surveys with a Piper SuperCub. Under proper conditions, early spring is the most efficient time for survey, and it also most accurately measures net annual recruitment. We counted similar proportions of the population during early spring surveys with the SuperCub as we did with the helicopter in either early winter or spring.

For best results, correct timing of these spring surveys is very important. The objective is to time flights such that the majority of deer are feeding on open ridges and south facing slopes where new green growth first appears. We obtained best results in flying when new growth of grasses and spring forbs had only recently started. The highest proportion of the population was observed in the open, and deer spent more time during the day in the open when flights were made before new growth had started under the forest canopy and before large amounts of new growth were available in open areas. Under these conditions, effective surveys can be flown during all hours of daylight except immediate mid-day.

Our data on deer distribution and dispersal patterns had important implications to the proper establishment of study areas and trend areas for measurement of population trend. When establishing these areas, marginal deer habitat must be included along with core habitat. On our study area,

population increases beyond a certain point were not measurable in core habitats. Much of the latter stages of population increase occurred in marginal habitat. In like manner, population declines generally occurred first and to the greatest extent in habitats marginal to core area. thus, trend areas that do not include marginal habitat may lack the capability to provide early warning of true population trend.

Age Structure and Sex and Age Ratios

Age structure was not useful in predicting population trends. It was most valuable in verifying past population history. Age structure has often been considered very important because it was easily collected at check stations, and little, if any, data were collected on population size or fawn recruitment. Often, the only information some states had on fawn recruitment was data for past years based on age structure of hunter-killed samples. Adequate sex and age classifications and population estimates provide better data for most management purposes than age structure from hunter-killed samples.

There are also other reasons, at least for populations in variable environments, why age-structural data may not be as useful to management as once thought. It has been commonly assumed in wildlife management that a hunted population has a younger age structure than an unhunted population. Similarly, healthy, growing populations had a younger age structure than unhealthy, high density populations. This was not necessarily the case in the Missouri River Breaks. It apparently was also not the case in some other northern Montana habitats. Data from the mule deer population on the Brinkman Preserve, which had been unhunted for many years (Rosgaard, unpubl. data), indicated a younger age structure than our hunted population.

The expectation that younger age structures occur in hunted populations may be partially valid for populations with stable recruitment rates. On average, hunted animals will not live as long as unhunted animals. Thus, the average age of adults should be less in hunted populations if recruitment is stable. However, where recruitment rates vary considerably from year to year, age structures may not differ measurably between hunted and unhunted populations.

A major reason why the assumption of a younger age structure for hunted populations does not hold for variable environments is its basis in the "principle" of compensatory reproduction. Because fawn survival on our study area was not directly related to number of deer in the population, a reduction in numbers by hunting did not necessarily result in increase fawn recruitment. Therefore, it was not surprising that age structure of the female population on our study area

was not younger during years of female harvest than during years when females were not harvested.

In comparing population ecology and dynamics among studies, care must be taken in expressing and interpreting various methods of reporting population composition. It is always most informative to be able to estimate and report total numbers in each category rather than report only ratios or percentages. This is especially true when determining the implications to management and to hunters. For example: assume that we implement a new season type and report that 10% of mule deer population was males last year and 14% was males this year. Did the new season result in an increase in survival of males? Not necessarily. The total number of males and females could have remained exactly the same, but fawn survival was much lower. Thus:

Year t	20	males (10%)
	100	females
	75	fawns
Year t+1	20	males (14%)
	100	females
	20	fawns

When examining the possibilities, it can be determined that survival of males could actually have declined under the new season even though they comprised a greater percentage of the population post season.

Similar problems exist when only ratios are reported. Assume we report that post-season fawn:doe ratios have remained at 70:100 for 3 years and the statewide hunter questionnaire has reported an exactly stable harvest of bucks, does, and fawns for each of the last 2 years. Have we achieved the manager's dream of stability and is everything wonderful? Possibly not! A potential result of observed stable levels of harvest and fawn recruitment in post-hunting season populations could be:

Year t - post season	20	males
	100	females
	70	fawns
	190	total deer
Year t+2 - post season	5	males
	65	females
	45	fawns
	115	total deer

Thus, stable numerical harvests and stable recruitment do not necessarily mean stable populations.

The main point of these examples is to show the pitfalls in the path of anyone making decisions based on data reported only as ratios or percentages. Estimates of population numbers or trend are almost essential for confidence in the meaning of ratios and percentages.

Interpreting Population Trend

Trends are one of the most widely used and abused tools of all aspects of life. If correctly used, trend information can be valuable, especially if data are sufficient to provide long-term perspective. When quick answers or decisions are required, we all usually rely on the trend ("Go with the trend" - "The trend is your friend"). However, trend data are also subject to misuse and overuse, and we often place too much confidence in its reliability.

At minimum, only 2 data points are required to establish a trend. Although most people are justifiably reluctant to place confidence in a 2 data-point trend, many decisions are based on no more than that. A longer-term data set is necessary to place annual changes in perspective. However, the particular data set or its specific length can greatly influence that perspective and the conclusions drawn.

Examples of both the value and the pitfalls inherent in trend data are illustrated by changes in numbers for the Missouri River Breaks mule deer population over time (Fig. 13.1). Five years of trend information, starting in 1960 (Fig. 13.1A), indicated that both short- and long-term trend for the population were up. However, addition of only 1 more year of data (Fig. 13.1B) indicated just the opposite conclusion; both short- and long-term trend were down. Expansion of the study to a "long-term" 10-year data set (Fig. 13.1C) indicated that, given a "longer-term" perspective, the "real" long-term trend was up. Again, however, once this uptrend was clearly established, the population immediately turned downward, and by 1975 after 16 years (Fig. 13.1D), the obvious trend was toward increased fluctuation, with higher highs and lower lows. After the lower low was established (1975), the population almost immediately began an uptrend (Fig. 13.1E). After 23 years, it appeared the trend for higher highs was coming to an end, but once again, one year of additional data (Fig. 13.1F) falsified trend projections by re-establishing the trend of higher highs. Finally, after 28 years (Fig. 13.1G), the trend of lower lows and higher highs appears to have been halted. Can we trust this interpretation of the trend? Is the population now fluctuating around a higher "equilibrium" level than that of the 1960s? A higher

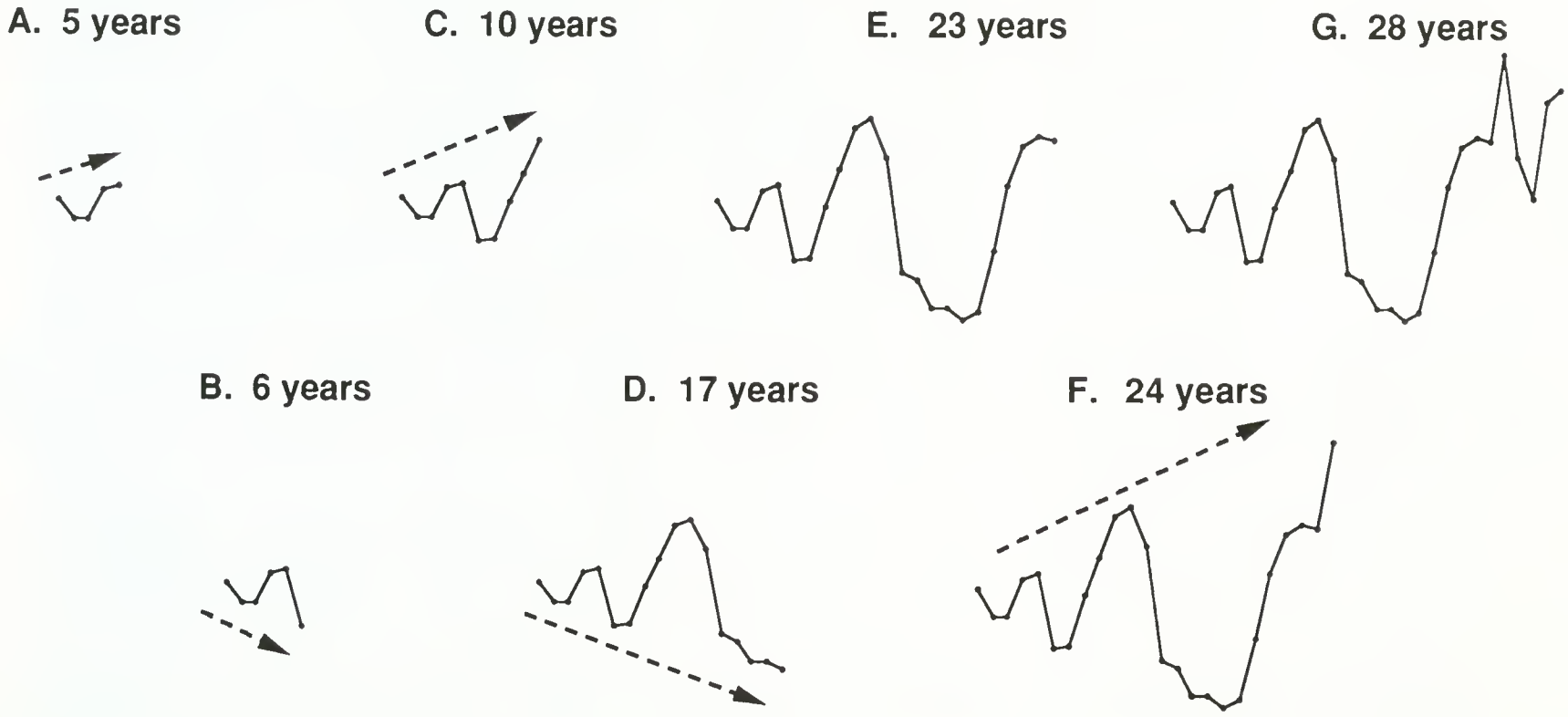


Figure 13.1. Trend in number of mule deer on the Missouri River Breaks study area over 5 (A), 6 (B), 10 (C), 17 (D), 23 (E), 24 (F), and 28 (G) year intervals, 1960-1987.

equilibrium level with reduced fluctuation has been a management goal after the 1970s. Whether that goal has been achieved and will be sustained can only be determined by additional years of testing.

Interpretation of trends and results and conclusions of studies may often depend upon such chance events as the particular year data collection starts and how long it continues. For example, for our study (Fig. 13.1G), the reader can choose a variety of 10 consecutive year periods that will indicate vastly different, even opposite, population trends. These could also provide vastly different interpretations of population ecology and regulation. The initial year of investigation makes all the difference in 10-year trend. Similarly, it is obvious that 10 years does not necessarily provide a long-term perspective. The degree of environmental variability within an area may be a major consideration in determining valid study length and reliability of trend projection.

One year's change did not make a trend, but at about the time a long-term trend seemed to become obvious, the trend was often about to change. This seemed to occur because extremes tended to make the past trend obvious and "extremes" were unlikely to occur for 2 or more years in succession. Thus, population or any other measured data tend to reverse after extremes.

We suggest that trends in 1 population on 1 area provide insight to dynamics only after long periods. To best or most quickly measure the results of any management practice, the trends of 1 "treated" and 1 "untreated" population within similar environmental types should be measured simultaneously. This paired population approach is necessary to determine how much of the trend was "natural" and how much resulted from management action.

Habitat Evaluation and Management

The importance of healthy, productive habitat to healthy, productive animal populations has been justly recognized for years. However, concurrence on the meaning of healthy habitat and habitat requirements of species is lacking. This results partly from the different perspectives and objectives of different individuals, groups, and agencies. It is also the result of the lack of solid information about and understanding of the interactions between habitat and animal populations despite years of various types of studies. The assumption that winter habitat ("range") was of overriding importance to big game populations in the northern United States may have resulted in inadequate data collection on other aspects of deer ecology. This led to lack of long-term

monitoring of animal-habitat relationships and confusion about those relationships. For example, despite millions of dollars spent on years of habitat manipulation including burning, cutting, chaining, spraying, plowing, planting, and etc., we are not aware of published data documenting benefits to big game populations in terms of survival or increased numbers. The lack of published information may indicate little or no monitoring of animal populations; perhaps it also indicates that beneficial results were not observed.

Some studies have shown that various animal populations have made increased or decreased use of treated areas, at least for a time. If increased use occurs, the assumption has usually been that the animals have benefitted. Documentation has remained lacking, however. Even much of the usage data is at best neutral or even negative about the effects of habitat manipulation on deer (Clarly et al. 1974, Short et al. 1977, McCulloch 1974). Cost effectiveness of these habitat manipulation projects is also questionable (Regelin 1975, Nellis 1977). In one of the few studies that measured population response to habitat manipulation, Klinger et al. (1989) found that, although black-tailed deer use of burned chaparral was temporarily higher, there was no significant change either in population density or fawn survival resulting from the burn.

The lack of definitive results from habitat management for deer may be related to multiple causes. Factors may include: 1.) lack of accurate knowledge about species habitat requirements; 2.) assuming too much knowledge (e.g., exclusive concentration on winter habitat/forage); 3.) larger home ranges of large mammals than small game result in manipulations impacting only a few animals; 4.) much of our effort is spent in trying to maintain existing habitat; and 5.) it is difficult to balance the requirements of multiple species and at the same time make changes sufficient to result in measurable benefits for 1 species.

Essentials of Mule Deer Habitat

Traditionally, the essence of habitat has been summarized as the amount and distribution of food, water, and cover (Dasmann 1971). For deer, emphasis has been almost entirely on food and most often on winter forage (see Chapter 1). Our data clearly show that plant phenology and forage quality are important to deer population dynamics. However, density-independent, rather than density-dependent factors played the greatest role in deer-nutritional relationships. Also, winter forage relationships were not of overriding importance; forage relationships during other seasons were of at least equal, and possibly greater importance. In this respect, Short (1981: p. 127) has summarized seasonal forage requirements well:

"Summer forage should allow adequate milk production by does and permit all deer to achieve adequate growth and fat storage. Autumn forage should be abundant and of good quality to delay the depletion of fat stores. Winter range should provide forage that minimizes energy deficits and fat depletion. Spring range should offer feed that permits early recovery from stresses of winter."

We view the first essential of mule deer habitat as space, a place to exist. Although this may seem basic or trite, it is important to establish that houses, highways, airports, parking lots, mines, other animals, etc. usurp space for living. Similarly, deep, drifted snow reduces space for living. Thus, not all space is usable throughout the year.

What types of space best provide for the requirements of mule deer? We found that mule deer were positively associated with topographic and vegetational diversity. Across their species distribution, mule deer occur in a wide variety of habitats and vegetation complexes. This is true even within Montana. Generally, however, relatively steep, broken terrain on at least a portion of the area is a common feature of all mule deer habitat.

Gentle terrain was uninhabitable by deer during severe winters on our study area. Rough terrain provided south-facing slopes that were relatively snow free and timbered north-facing slopes that provided thermal cover and uncrusted, undrifted snow cover of lesser depth than on open areas. Rough terrain also helped provide vegetational diversity and microclimatalogical diversity which provided forage diversity and extended the period of availability of succulent forage during late summer and autumn. Habitat diversity also interacted with the social system of mule deer to provide more parturition territories in more diverse areas. Rough terrain and thick timber limited hunter access, thereby increasing security for deer. It also provided mule deer better hiding and escape cover from coyotes by limiting the ability of coyotes to maintain visual contact with the deer. Overall, physiographic and vegetational diversity provided the best natural system to provide quality forage for the longest periods. It also provided more alternative use areas to compensate for the variety of environmental and man-induced events that occurred.

Often ecological reports spend many pages discussing animal use of and importance of specific habitat-land types. We will not do that here. Rather, to understand and affect mule deer population dynamics, we believe it more important to understand why mule deer used some types more than others and some at different times than others. As noted previously, mule deer live in a variety of environments, thus the specific

type is of less importance than the function it provides. Effective management, even on a specific area, needs to be based on the why of use, not just the fact of use.

At some point in time, for some purpose, mule deer used all vegetation types on our area. The importance of some types or sites to the long-term health of the mule deer population was evident in some cases only after long-term monitoring. Assenting to the "sacrifice" of some of those areas based on limited data could have detrimental effects on the population over the long-term.

Mule deer on our study area appeared to strongly prefer Douglas fir habitat types yearlong. However, Douglas fir habitat was absent from the eastern portion of our study area and further east in Montana. Obviously, mule deer in those areas somehow survive and even thrive in the absence of Douglas fir. Similarly, mule deer on our study area seem to survive without the rocky outcrops prevalent on many Ponderosa Pine winter ranges in western Montana. Thus, deer prefer certain areas or types at certain times for what they provide rather than what they are. On our study area, Douglas fir types are relatively moist types within a drought-prone environment. Where available, they provide hiding cover and succulent forage during summer and autumn and thermal cover, lower snow depths, and softer snow during winter. All of these contribute toward the attainment of a positive energy balance on an annual basis.

As noted earlier, mule deer live well on many areas without Douglas fir types. Something(s) else obviously substitutes for the Douglas fir types and fulfills its function in maintaining a positive energy balance for deer. A common substitution factor in much of central and eastern Montana is agricultural forage. Many crops, such as alfalfa, remain succulent longer than natural forages. Others, such as barley, corn, or sugar beets provide higher energy forage than naturally available. These forages are also more dependable than natural forages. Enough may be available for deer even when drought results in an economic crop failure for the farmer or rancher. Thus, these high quality, high energy agricultural crops can often substitute for a lesser degree of thermal cover, for example. In most "natural" situations, there is an interaction between forage and cover in the energy balance equation. That is, adequate thermal cover during winter can help ameliorate the lack of quality forage because it helps reduce energy use. Similarly, availability of high quality agricultural forage may ameliorate the absence of adequate thermal cover.

The importance to deer populations of small, seldom used areas or types and areas that often received use for a very

limited time was evident from this study. This type of information would seldom be discovered during short-term investigations. For example, for about a month during April, mule deer would occasionally bed within the Douglas fir type, but feed almost exclusively within the Sagebrush-Grassland, Shale-Artemisia, or other open types. The latter are the first sites on which new, succulent green forage becomes available. Thus, substantial use of these types for only 1 month out of 12 may significantly increase the energy balance equation of the deer.

Similarly, data collected during the severe winters of 1977-78 and 1978-79 (Chapter 8) indicated that small, seldom used areas provided "critical" winter range during those years. The importance of those areas certainly could not have been predicted based on the poor quantity and quality of forage on the sites.

Our interpretation of the relative importance of habitat types and areas is vastly different from that usually inherent in the "key species-key area" concept. A variety of areas and types were critical to survival of deer over time. Except on a frequency of operation basis, one could not be separated out as more critical or "key" than another. Some were "critical" every year, but others, perhaps critical only once every 10 years, were just as necessary to long-term survival of existing deer populations.

Allowing oneself to be badgered into designating certain areas as more critical than others by resource development-extraction agencies or groups results in sacrifice of areas which can be of equal importance. The sacrifice of areas that are of less frequent critical importance leads to insidious long-term declines or declines that may occur abruptly long after the causative event.

The essentials of mule deer habitat, then, are a place to live and adequate diversity to provide options for maintaining a positive energy balance. In the natural environment, we cannot over-emphasize the preservation of diversity. Deer populations will fluctuate with the environment, but diversity will ensure that any one event is less likely to be catastrophic. Population characteristics and dynamics will generally follow diversity. The greater the diversity in an environment, the more stable the dynamics. Populations with fewer options to counter severe environmental events will be subject to wider fluctuations.

Dynamics can also be stabilized by the "domestication" of intensive management. For more intensively managed situations, there are substitutes for natural diversity. We can, for example, raise deer in pens in parking lots by

feeding them appropriate forage and employing veterinarians. We can also enclose by fence and selectively cull animals, essentially simulating domestic livestock operations. These latter options, however, do not appeal to many people.

Habitat Maintenance, Enhancement, and Development

As can be surmised from our previous discussions, we believe that maintenance of diversity is important to mule deer. Deer are very effective at taking advantage of situations, areas, etc. that increase their chance of survival. In habitat management, it seems important that we leave them as many options as possible. Earlier in the century, increased diversity could often be provided by various land uses (e.g., timber cutting or agricultural development). As is typical, however, very little of anything is done in moderation. Increasingly, diversity has peaked as we passed from diversity that included some natural monocultures to an increasing proportion of manipulated monocultures. Thus, habitat management by necessity has increasing become "anti development", promoting maintenance of existing habitat rather than additional "development" or "enhancement".

Given the lack of a proven beneficial track record by previous "habitat development" projects, we are reluctant to specifically recommend many manipulative developments. Also, increased ecological knowledge gained by this study and others has cast doubt on the necessity, benefits, or cost-effectiveness of many manipulations. Certainly, preserving winter range space by precluding subdivision will provide meaningful long-term benefit, but attempts to increase forage quantity for deer on winter range may not produce measurable benefits.

Generally, both the stable and variable properties of the environment are difficult to change, especially to benefit species such as mule deer. In some situations, however, we believe our knowledge is sufficient to recommend potential improvements for mule deer habitat. The applications of these suggestions will depend, among other things, upon the importance of and goals for other species in the area.

In most cases, alteration of topography is uneconomic and impractical. However, in cases where proposed mining activities will move large amounts of overburden, reclamation of the site could be done in ways that might benefit mule deer. Most mining reclamation plans require that the site be restored to its original contour or possibly to even less topographic relief than originally occurred to reduce potential erosion. We proposed that if it is desirable to benefit mule deer, the overburden could be deposited,

oriented, and contoured in such a way that topographic diversity and specific exposures were more advantageous to mule deer after mining than before. Erosion potential could be addressed by various techniques with the understanding that some degree of erosion is natural and helps add to diversity of slope and exposure.

Similarly, planned fires may alter the habitat structure in ways beneficial to mule deer. Burned Douglas fir-juniper habitat type was preferred by mule deer on this area during summer-winter. Only very limited burning of small patches of that type are recommended, however, because mule deer make important use of thickly timbered Douglas fir-juniper habitat during severe winters. Also, Rocky Mountain elk, a species of great interest and concern on the area, require these thickly timbered areas for security during hunting season.

The planting and maintenance of alfalfa in small patches throughout public lands in arid eastern Montana would probably be beneficial to mule deer. This nutritious legume, with its extremely well developed root system, is competitive for water and generally remains green and succulent longer than most native forage species. The availability of alfalfa would increase the length of time that quality forage was available to mule deer in many areas and years. It also would provide more stable, dependable forage, potentially resulting in less population fluctuation. Additionally, planting alfalfa on public lands within deer habitat and/or at the margin of public deer habitat and adjacent private agricultural lands could act as a lure crop, reducing deer damage to private agricultural crops during dry years.

Based on the data of Mackie (1970) and this study, we do not believe that further water development within the riverbreaks habitat will benefit mule deer. Adequate water sources seem to exist, and further development could only result in increasing overlap between distributions of cattle and mule deer. Lewis and Clark as well as other "oldtimers" present before 1905 reported "vast" numbers of mule deer in the riverbreaks before any water development occurred.

Generally, some degree of cattle grazing has likely been beneficial to mule deer habitat values over the long term. Locally, and for some shorter term periods, it has probably been detrimental. For example, some information presented in this report (Chapters 7, 8, and 9), indicated that heavy early spring grazing by cattle might be detrimental to mule deer. To benefit mule deer, we recommend that spring grazing by cattle be deferred to as late a date as possible.

Intensity of grazing by domestic livestock has varied tremendously over the years, but stocking rates have generally

been much more reasonable in recent years than earlier. We believe that as long as overall grazing pressure by domestic livestock is light to moderate, the existing season-long grazing system provides a patchwork of diversity, including heavily grazed, moderately grazed, lightly grazed, and ungrazed areas within the Breaks type. This diversity results in a wide variety of plants species adapted to each situation. The wider the variety, the greater the spread of maturation dates and the more likely some species of value to deer will occur under all environmental conditions. Both totally ungrazed and heavily stocked areas would likely result in lower diversity.

Similarly, highly managed, "efficient beef production grazing systems", often also promoted as good for vegetation and soil may also result in monocultural vegetation patterns. This, together with increased social disturbance associated with intensively managed systems, would likely be detrimental to mule deer.

Finally, we caution that where riparian habitats comprise an important portion of an area, conclusions about appropriate grazing systems might be different than for "Breaks" habitat type.

APPENDIX A

Appendix A. Arithmetically modeled population estimates for mule deer on the Missouri River Breaks study area, 1960-1987.

Period	Total	Adults	Fawns	Females	Males
October 1960	1225	785	480	535	250
December 1960	955	570	385	445	125
May 1961	925	555	370	435	120
				185	185
				620	305
October 1961	1235	925	310	620	305
December 1961	850	645	205	435	210
May 1962	805	615	190	415	200
				95	95
				510	295
October 1962	1055	805	250	510	295
December 1962	850	620	230	410	210
May 1963	810	590	220	390	200
				110	110
				500	310
October 1963	1295	810	485	500	310
December 1963	1000	640	360	430	210
May 1964	910	620	290	415	205
				145	145
				560	350
October 1964	1260	910	350	560	350
December 1964	1020	720	300	490	230
May 1965	715	645	70	440	205
				35	35
				475	240
October 1965	895	715	180	475	240
December 1965	725	575	150	420	155
May 1966	670	545	125	400	145
				60	65
				460	210
October 1966	920	670	250	460	210
December 1966	730	510	220	385	125
May 1967	665	485	180	365	120
				90	90
				455	210

Appendix A. (Continued)

Period	Total	Adults	Fawns	Females	Males
October 1967	1100	665	435	455	210
December 1967	935	535	400	400	135
May 1968	825	505	320	375	130
				160	160
				535	290
October 1968	1335	825	510	535	290
December 1968	1080	640	440	465	175
May 1969	870	585	285	425	160
				140	145
				565	305
October 1969	1480	870	610	565	305
December 1969	1250	705	545	505	200
May 1970	1070	670	400	480	190
				200	200
				680	390
October 1970	1530	1070	460	680	390
December 1970	1290	865	425	620	245
May 1971	1140	800	340	575	225
				170	170
				745	395
October 1971	1510	1140	370	745	395
December 1971	1130	825	305	610	215
May 1972	665	595	70	425	170
				35	35
				460	205
October 1972	830	665	165	460	205
December 1972	675	535	140	380	155
May 1973	600	485	115	335	150
				55	60
				390	210
October 1973	780	600	180	390	210
December 1973	640	470	170	320	150
May 1974	565	440	125	295	145
				60	65
				355	210
October 1974	685	565	120	355	210
December 1974	535	430	105	295	135
May 1975	470	395	75	275	120
				35	40
				310	160

Appendix A. (Continued)

Period	Total	Adults	Fawns	Females	Males
October 1975	695	470	225	310	160
December 1975	535	395	145	310	85
May 1976	390	355	35	275	80
				15	20
				290	100
October 1976	565	390	175	290	100
December 1976	490	365	125	280	85
May 1977	435	335	100	255	80
				50	50
				305	130
October 1977	675	435	240	305	130
December 1977	520	365	155	300	65
May 1978	450	355	95	290	65
				45	50
				335	115
October 1978	800	450	350	335	115
December 1978	760	420	340	325	95
May 1979	640	390	250	300	90
				125	125
				425	215
October 1979	1135	640	495	425	215
December 1979	1020	530	490	420	110
May 1980	910	500	410	400	105
				150	205
				550	310
October 1980	1355	860	495	550	310
December 1980	1175	685	490	540	145
May 1981	1080	670	410	530	135
				150	205
				680	345
October 1981	1555	1025	530	680	345
December 1981	1215	745	470	600	145
May 1982	985	685	300	550	135
				150	150
				700	285
October 1982	1490	985	505	700	285
December 1982	1200	715	485	590	125
May 1983	1115	700	415	580	120
				210	205
				790	325

Appendix A. (Continued)

Period	Total	Adults	Fawns	Females	Males
October 1983	1715	1115	600	790	325
December 1983	1545	1020	525	775	245
May 1984	1040	920	120	700	220
				60	60
				760	280
October 1984	1365	1040	325	760	280
December 1984	1135	895	240	705	190
May 1985	870	830	40	655	175
				20	20
				675	195
October 1985	1075	870	205	675	195
December 1985	975	785	190	665	120
May 1986	915	775	140	660	115
				70	70
				730	185
October 1986	1480	915	565	730	185
December 1986	1355	805	550	715	90
May 1987	1230	760	470	675	85
				235	235
				910	320
October 1987	1720	1115	605	795	320
December 1987	1405	850	555	695	155
May 1988	1200	810	390	665	145

Appendix B

Table B1. Method of calculating estimated forb production on the study area using 1982 as an example.

Year	Vegetation Type	Total Area (ha)	Usable Area (ha)	Relative Abundance Coum[a]	kg/ha Coum	Total kg Coum
1982	AA[b]	10,328	6,899	1.00	47	324,253
	PJG	5,106	4,883	0.39	18.3	89,359
	PJS	4,024	3,955	0.00	0	0
	DFJ	3,591	3,515	0.00	0	0
	GW and SA	1,796	1,524	0.06	2.8	4,267
	All others	2,555	1,988	0.00	0	
					417,879	
				Relative Abundance Meof	kg/ha Meof	Total kg Meof
	AA		6,899	1.00	26.4	182,134
	PJG		4,883	2.42	63.9	312,024
	PJS		3,955	0.23	6.1	24,126
	DFJ		3,515	2.08	54.9	192,974
	GW and SA		1,524	1.62	42.8	65,227
	All others		1,988	1.00	26.4	52,483
					828,968	
				Relative Abundance Other Forbs	kg/ha Forbs	Total kg Other Forbs
	AA		6,899	1.00	158	1,090,042
	PJG		4,883	0.23	36.3	177,253
	PJS		3,955	0.02	3.2	12,656
	DFJ		3,515	1.09	172.2	605,283
	GW and SA		1,524	0.17	26.9	40,995
	All others		1,988	0.17	26.9	53,477
					1,979,706	
					TOTAL KG ALL FORBS	
					3,226,553	

[a] For plant name abbreviations, see Appendix C.
[b] For vegetation type abbreviations, see Table 3.2 and 3.3.

Table B2. Method of calculating estimated shrub production on the study area using 1982 as an example.

Year	Vegetation Type	Total Area (ha)	Usable Area (ha)	Relative Abundance Rhar[a]	kg/ha Rhar	Total kg Rhar
1982	AA[b]	10,328	6,899	0.00	--	--
	PJG	5,106	4,883	1.00	25	122,075
	PJS	4,024	3,955	0.11	2.8	11,074
	DFJ	3,591	3,515	1.00	25	87,875
	GW and SA	1,796	1,524	0.00	--	--
	All others	2,555	1,988	0.00	--	--
						221,024

Vegetation Type	Usable Area (ha)	Relative Abundance Rosa	kg/ha Rosa	Total kg Rosa	Relative Abundance Symp.	kg/ha Symp.	Total kg Symp.
AA	6,899	0.04	2.1	14,488	0.00	--	--
PJG	4,883	1.39	74.4	363,295	0.36	5.9	28,810
PJS	3,955	0.15	8.0	31,640	0.01	0.2	791
DFJ	3,515	1.00	53.5	188,052	1.00	16.5	57,998
GW and SA	1,524	0.04	2.1	3,200	0.00	--	--
All others	1,988	0.00	--	--	0.00	--	--
				600,675			87,599

Vegetation Type	Relative Abundance Prvi	kg/ha Prvi	Total kg Prvi	Total kg All Shrubs
AA	0.00	--	--	
PJG	0.11	4.7	22,950	
PJS	0.00	--	--	
DFJ	1.00	42.5	149,387	
GW and SA	0.00	--	--	
All others	0.00	--	--	
			172,337	1,081,635

[a] For plant name abbreviations, see Appendix C.
[b] For vegetation type abbreviations, see Table 3.2 and 3.3.

Appendix C. Common and scientific names of plants for which abbreviations are occasionally used in tables.

Abbreviation	Common Name	Scientific Name
Artr	Big sagebrush	*Artemisia tridentata*
Chna	Rubber rabbitbrush	*Chrysothamnus nauseosus*
Chvi	Green rabbitbrush	*Chrysothamnus viscidiflorus*
Coum	Bastard toadflax	*Comandra umbellata*
Jusc	Rocky Mountain juniper	*Juniperus scopulorum*
Meof	Yellow sweetclover	*Melilotus officionalis*
Pipo	Ponderosa pine	*Pinus ponderosa*
Prvi	Chokecherry	*Prunus virginiana*
Psme	Douglas fir	*Pseudotsuga menziesii*
Rhar	Aromatic sumac	*Rhus aromatica*
Ribes spp.	Currant and Gooseberry	various species
Ronu	Nootka rose	*Rosa nutkana*
Rosa spp.	Rose	various species
Syoc	Western Snowberry	*Symphorocarpos occidentalis*
Symp. spp.	Snowberry	various species

Appendix D. Excerpts from quarterly narratives of CMRNWR personnel and DFWP reports, 1940-1959.

1940 - "The western end of the Range [present study area] is the only high grade deer country. ...but, deer are scarce."
- "Rabbits are on the upswing of the cycle."
- "No plan has as yet been even tentatively set up for predator control."

1941 - "Mule deer though scarce, may be increasing a little."
- "Everything indicates a small upswing in mule deer production."
- "We rarely see deer, though my contacts with several coyote trappers who work within or near our boundaries indicate that deer are definitely increasing."
- "Range conditions for big game are ideal as to forage in the range as a whole."
- "In spite of tremendous numbers of coyotes being taken, I have seen twice as many coyotes as I saw last year."
- "Both Lepus and Silvilagus [sic] are picking up. The latter look as if they may be approaching a cycle peak now. Mice, we repeat are numerous, and jackrabbits as well as cottontails are on the upgrade. In the country in general, however, jackrabbits have been hunted extensively for their skins, which have been worth up to $0.42 each."

1942 - "It is obvious that a good population of blacktailed [sic] deer exist on the Game Range. Contacts with stockmen and farmers living near the Game Range indicate that this population is and has been increasing through the last three or four years."
- "With weather conditions as they have been for the past four years, range conditions are at present better than at any time within the memory of the old-timers."
- "Coyotes are frequently observed."
- "Numerous complaints were received through this report period relative to the abundance and damage being done to sheep [domestic] by coyotes."

1943 - Text in a 1943 report, along with an enclosed map, indicated that 1.3 mule deer per square mile were estimated for the portion of the Game Range including the present study area. This was the highest estimated density for the Game Range. However, no indication was provided as to how these figures were derived.

- "We have continued to receive complaints of an excessive population of coyotes on the Game Range from livestock operators around the area."

1944 - "Range conditions were excellent and animals observed through this period were in excellent condition."
- "Conditions for deer through this period were ideal."
- Holibaugh (1944), after a reconnaissance trip in the vicinity of our present study area, stated: "It also becomes more evident with each trip into the breaks country that the deer herd is increasing at a tremendous rate... Deer are abundant, sufficiently so to be a good hunting unit."
- "On October 20, Mr. DuBeau and myself worked out one of the tributaries of Sand Creek located in Sections 23, 24, 25, and 26, Township 21 North, Range 24 East [on the present study area]. Approximately four square miles were intensively covered. This included the main stream and all of the wooded coulees tributary to it. Thirty-one different mule deer does and three different mule deer bucks were observed in this area. It is estimated that between 60 and 70% of the deer in the area were observed."

[Author's Note:] The 8.5 mule deer/mi^2 observed in 1944 indicated a high deer population by that time. The actual density may have been higher. Although people making a deer drive through an area may recount the same deer more than once, it is also likely that they miss many deer (McCullough 1979). Aerial observations during autumn 1979-1986 on this same 4 mi^2 area indicated 17-31 mule deer (4.3-7.8/mi^2) observed per flight. Observability indexes (Lincoln Indexes) during the same period indicated that actual densities ranged from 11 to 17 mule deer/mi^2. It is possible that mule deer density on this area was quite similar during 1944 to densities observed during 1979-1986.

1945 - "Mule deer - Trend up. Range excellent."
- "The coyote population has become unusually heavy over the past 5 years."
- "The low price of coyote pelts, two to five dollars, along with a critical labor shortage, probably has been the cause of a constant uptrend in the population of coyotes over all of eastern Montana."

1946 - "Mule deer - Trend is a strong up over all of the Game Range. Carrying capacity of the Game Range in Petroleum, Fergus, and Phillips Counties will have to be closely watched if a dry cycle starts, as our population here is high."
- "It appears as tho [sic] part of the range in Phillips, Fergus, and Petroleum Counties should be

opened to hunting within the next two or three years."

- "Jackrabbits - Trend is no longer down, but believed now to be steady, with an increase probable."
- "Coyotes - Trend still up, with a brighter future. More effective control is now possible since more men are available."
- "It is believed that we loose [sic] many deer each year to coyotes but since their population is high enough to withstand extensive depredation, they still increase."
- "We are pleased to announce for the first time that an intensive coyote control program is underway." (September-December, 1946).
- "The program planned was a duplicate of the one conducted in Nevada in 1945-46, and consisted of the distribution of small cubes of strychnine enclosed in a small ball of horse tallow which was coated on the outside with sugar. This is called a poison pill. Distribution was accomplished by plane for economy in funds and efficiency in operation. Plans were made to poison the entire Game Range area and 1,200,000 acres adjacent to it."
- "Manufacture of the poison pills started about the first of November and by the end of the first week production was up to about 9,000 per day, for the three man crew."

1947 - "The first extensive control of these [coyotes] was done through the winter, through the use of poison distributed by airplanes. Results in the areas treated were above expectations. A conservative estimate of the poison kill stands at 1,500."

- "Mule Deer - Trend is rapidly up on the west end ... The population on the western thirty miles of the Game Range [includes the present study area] is nearing the point of critical forage consumption, indicating the necessity of an open season soon."

[Author's Note:] The first substantial quantitative data on mule deer population size on the area were collected by aerial census during September, 1947 (Brown 1947). Brown and an observer in a fixed-wing aircraft flew 40 miles of strip census lines in northeast Fergus County, including our study area. They counted 48 mule deer and assumed that they had observed deer within a 1/4-mile-wide strip for a total of 10 square miles of coverage. These data convert to an observed density of 4.8 mule deer/mi^2 (1.85/km^2). Our observability indexes for fixed-wing aircraft surveys during autumn have ranged from 0.265 to 0.488 (see Chapter 4). Because Brown (1947) noted that the " air was extremely rough," the percentage of the deer present that was observed at the time

of their flight was probably at the lower end of the range. The application of the observability factor to their data indicates a density of 18 mule deer/mi^2 (4.8/0.265). This figure probably should be corrected again because the area they flew was that which, in recent years, had the highest density on the study area. Data collected from 1964-1986 indicated that the density figure from Brown (1947) should be multiplied by a correction factor of 0.70 to convert to a figure applicable to the entire study area. This final conversion indicated a density of 12.6 mule deer/mi^2 (4.86/km^2) for September, 1947.

1948 - "The statement that continual outflux of deer from the Game Range is seeding all of Eastern Montana is heard many times from many quarters. Leo Coleman who was there when 2 men killed one of the last Grizzly Bears on the Game Range in the Timber Creek breaks in 1905 states emphatically that there are many more deer along the river in the Game Range than at any time in their memory. This statement is always agreed upon by old-timers."

- "Our deer population on many areas is nearly to the point where 50% of the annual growth on the most palatable species is being used by wildlife. Deer populations must be watched closely to prevent range damage. The time is not too far distant when the unmentionable proposition of opening the season on does <u>will</u> <u>have</u> to be discussed."
- "All animals observed and checked were in fine condition with fine glossy coats. Bucks handled were all free from external parasites and loaded with fat."
- "One remark common to all livestock operators and old timers is, "This years crop of antelope [or deer] fawns is the largest crop of twins I have ever seen." It is believed that last winters 1080 program is responsible for the quotation."

[Author's Note] It is likely that the coyote poisoning program initiated during winter 1946-47 did result in increased fawn survival. There was little consistent information, with large sample sizes, available for fawn/female or fawn/adult ratios prior to 1949. However, narratives indicated that pronghorn antelope fawn/adult ratios increased from an "average" of about 0.3 fawns/adult prior to coyote poisoning during winter 1946-47 to 0.63 fawns/adult during 1948. The narratives implied that fawn/adult ratios for mule deer increased to a like or greater degree. The fawn/100 female ratios reported for mule deer during 1949-1956, indicated consistently higher fawn/100 female ratios than observed during any other time period.

[Author's Note:] Another strip census flight covering an estimated seven square miles on the study area was flown on 24 February, 1948. Brown (1948) observed 40 mule deer (5.7/mi^2 observed) and estimated that "it is possible that not more than 50% of deer in this area were observed." The estimate of 50% observability for that time of year from a fixed-wing aircraft is reasonable, based on our more recent work. Again, the area flown was what is presently high density habitat, and we applied a correction factor that indicated a density of eight mule deer/mi^2 (3.09/km^2). The September, 1947, and February, 1948, estimates appear to be consistent with each other, especially when considering autumn and overwinter mortality. We believe that eight to 12 mule deer/mi^2 (3.1-4.6/km^2) represents a reasonable minimum density estimate for early winter, 1947-48.

[Author's Note:] The first hunting season for bucks in 12 years within the CMRNWR was held during autumn 1948. The season had been open for bucks since 1933 on areas off the CMRNWR. Checking stations for hunters were established for the first two days of the season on two roads leading to the study area. The 36% hunter success rate recorded for the opening two days compares favorably with opening day success rates in 1960-64 (20-47%) and 1979-80 (23-26%), when deer populations were at preseason levels of 10-13+/mi^2. That further substantiated a population estimate of 8-12 deer/mi^2 during February 1948.

1949 - "All deer killed were in excellent condition and almost every hunter had some comment on how fat his buck was."
- "Although we experienced one of the most severe extended winters for many years, we have no evidence to dispute our casual observations, and information from local residents on and near the Game Range, to the effect that our game animals came through the winter in good condition and with very little loss."
- "Practically no coyotes, or the effects of them, have been noted on the Refuge. Nearly all local livestock men and sportsmen speak highly of the progress made in coyote eradication.
- "Jackrabbits and cottontails - Both are increasing considerably, especially the cottontail which seem to be almost everywhere."

[Author's Note:) A sample of 144 mule deer classified during early winter, 1949-50, indicated 96 fawns/100 females. That high level of fawn production and survival indicated little initial impact of the severe winter of 1948-49 on the 1949 fawn cohort.

1950 - "Reports of heavy deer losses on the Game Range and vicinity have been investigated and almost without exception we find these reports to be greatly exaggerated..." (winter 1949-50)

- "Upon receipt of reports from the Hedman Brothers, local ranchers in Petroleum County in mid-March that winter loss of deer in that area was extremely heavy and would probably amount to 30 or 40 percent of the fawns and yearlings, we again conducted an aerial survey in Petroleum County on March 30 through cooperation of Don Brown and the State Fish and Game Department. Therefore, a resurvey was made of the entire area and the count came out so close to that of the previous census in February and due to the fact that only one dead deer was seen from the plane, we came to the conclusion that the loss could not be nearly so heavy as reported."
- "It is quite possible that winter losses in certain localities of the Game range may have been heavier last winter than was indicated in previous reports." (summer-fall 1950)
- "The most noticeable fact is that many of the [deer] fawns were dropped later than usual this summer." (May-August 1950).
- "At the close of the report period [Aug. 1950], a high percent of the fawns are still heavily spotted. We feel that the exceptionally severe past winter is closely tied in with this fact."
- "Coyotes - The time is here when this species could be dropped from mention in the Narrative Report. They are now reduced to such an extent on the Game Range that observing one is cause for special comment."

[Author's Note:] An aerial mule deer census was again conducted during early February 1950. Viewing conditions were good because of 16 inches of snow on the ground. The survey area was larger than that of previous surveys and included areas that, at present, have mule deer densities about half that on the study area. One hundred thirty-two (132) mule deer were observed on 157 miles of strips that covered an estimated 39.25 mi^2. Observed density was 3.4 mule deer/mi^2. If 50% of the mule deer present were observed, the estimated density was 6.7/mi^2. If mule deer density distribution was the same in 1950 as at present, then the density estimate for our current study area may have been higher, at about 8-10/mi^2. We believe that 7-10 mule deer/mi^2 (2.7-3.9/km^2) is a reasonable estimate for February 1950. The recensus flown on 30 March, 1950, apparently had nearly the same results, but the data for that flight were not found. These data indicated a probable decline in density, compared to 1947-48. Such a decline is reasonable because the February 1950 census occurred after the severe winter of 1948-49 and during the

severe winter of 1949-50. The narratives indicated the probability of winter loss, at least during 1949-50.

1951 - "Food and cover conditions for big game on the area are excellent."

[Author's Note:] The final census flight of the 1950s was flown on 13 February, 1951. Sixty-eight miles of strips were flown, covering an estimated 16 mi^2. Eighty mule deer were counted and, assuming a 50% efficiency of observation, a density estimate of 10 mule deer/mi^2 (3.86/km^2) was indicated.

[Author's Note:] Classifications for population composition were made during both early October and early December, 1951. For 519 mule deer classified during early October, 125 fawns/100 females and 86 adult males/100 females were observed. It is likely that classifications made during the first week of October somewhat overestimated the proportion of males in the population. For 470 mule deer classified during early December, 125 fawns/100 females and 38 adult males/100 females were observed. If there were around 10 mule deer/mi^2 during spring 1951, then the observed level of fawn production and recruitment, by itself, would have resulted in pre-hunting season populations of 15-18 mule deer/mi^2. Based on data from hunter checking stations and post-season questionnaires, we estimate that the number of mule deer harvested on the study area was 200-300. Mule deer population density during December 1951 may have been in the range of 12-15/mi^2.

1952 - "There is every indication that our mule deer herd is one of the healthiest and most productive in the country. While there aren't any widespread signs of overuse as yet, we should be constantly on guard,"...
- "Bobcats are probably the most numerous predator on the Game Range. Their numbers are far above normal on the west end of the area in the most heavily populated big game locality."

[Author's Note:] Pre-hunting season classification of 1,191 mule deer during 1952 indicated that there were 94 fawns/100 females and 48 adult males/100 females. A post-season classification of 860 mule deer was comprised of 91 fawns/100 females and 29 adult males/100 females. Data from hunter checking stations and post-season questionnaires indicated that 250-350 mule deer may have been harvested from the study area. An estimated 791 mule deer were harvested from the northern end of the county, with much of the pressure directed toward the vicinity of the study area.

1953 - "Due to favorable weather conditions during the spring and early summer, grasses, weeds, herbaceous plants, trees, and shrubs all made an excellent growth." ...

"the leaves and seed heads on many species remained green and succulent for a much longer than normal period."

[Author's Note:] Reports of widespread deer mortality during late summer and autumn, 1953, especially along the Missouri River, were investigated (Chaffee 1954). Based on more recent information and experience, we believe that the reported mortality during summer and autumn, 1953, represented an outbreak of epizootic hemorrhagic disease (EHD). During more recent years, mortality from EHD has been mostly confined to white-tailed deer and few mule deer have died. At least some mule deer living near the Missouri River died during late summer and autumn, 1953, but it is unlikely that the outbreak of EHD had a major impact on mule deer populations.

1954 - "The mule deer population in the areas that have been open to hunting, is lower than at any period since 1949."
- "All browse species, as well as grasses and weeds, made an excellent growth this season."
- "Game range personnel have seen only 2 Coyotes this period. The bobcat population over the entire area is believed to be high." (May-Aug. 1954)
- "A total of 6 coyotes were observed on the Game Range this period [Sept.-Dec. 1954]. This is the largest number recorded in any period report since 1949. There have been two complaints of coyote depredation on domestic sheep bands running in or adjacent to the Game Range this period."

[Author's Note:] During August, 112 fawns/100 females were observed, and a classification of 684 mule deer during October indicated 94 fawns/100 females.

1955 - "The latter part of the summer was extremely dry"...
- "Coyotes - This animal is definitely on an increase on the Game Range but are by no means present in alarming numbers. Our personnel have seen as high as four animals in one day."

[Author's Note:] During August 1955, 128 fawns/100 females were observed.

1956 - "When drought conditions occur over a large area as they have during the past two seasons, the deer tend to concentrate within a five to six mile strip along the river or reservoir."
- "This movement back to the river breaks was first noticed in locally dry areas late in the fall of 1955."

- "Mule deer range showed some signs of over-use in the vicinity of the game range boundary and along the heads of the many drainages at a considerable distance back from the river. As is normally the case, during periods of severe drought and poor market, livestock operators find it difficult to reduce their herds to the carrying capacity of the range. Heavy use by livestock results in utilization of browse species not normally consumed during the regular grazing season."
- "When ranges outside [the Game Range] are overutilized by livestock during drought periods such as we have experienced in the past two years, both cattle and sheep utilize most, if not all, of the preferred browse species even during the summer months forcing game onto other ranges."
- "At the extreme west end of the game range, [our study area] grasses and sedges made no growth whatsoever this season or for that matter we can also include the season of 1955."
- "A few more coyotes have been observed on the area this period than for a number of years. Hunters during the deer season have likewise reported seeing more coyotes than in the past. Complaints are more frequent from sheep operators in or near the game range."
- During August, 116 fawns/100 female mule deer were observed.

1957 - "A number of mule deer checked were not in as good condition as in previous years and a few animals were found to be thin and a considerable number harbored lice."
- "During the report period a control campaign has been undertaken to clean up or at least reduce the population of predators in that section of the Game Range lying west of the mouth of the Musselshell [includes our study area]. The PARC trapper on the south side of the river either poisoned with 1080, killed with cyanide or trapped a total of 54 coyotes and 19 bobcats during the period [September-December 1957]."
- "The rabbit population, especially the jackrabbit, is down to the lowest point in game range history. It is becoming a rare occurrence when personnel report seeing a jack".

1958 - "In our opinion, deer generally, as well as other big game species present, suffered to a considerable extent from lack of water and were probably in poorer physical condition at the end of the report period [January-April] than during any winter since the Game Range was established."

- "... dried-out range lands did not offer a very succulent diet." (May-August).
- "On the West Unit, a long arid summer resulted in many waterholes and reservoirs drying up"... (Sept.-Dec.)

[Author's Note:] During February 1958, an attempt was made to remove all deer from a 8.13 km^2 pasture that had been fenced to receive a transplant of Rocky Mountain bighorn sheep (Janson 1958). This pasture was approximately 9.7 km west of the study area and within similar habitat. Fourteen mule deer were shot, two were known to have escaped through the fence, and a minimum of eight deer were known to have survived and remained in the pasture. These data provided a minimum density estimate of 7.7 mule deer/mi^2 (2.95/km^2) for an area near our study area during February 1958.

1959 - (Jan.-Apr.) ..."Severe winter conditions and particularly deep snow caused hardship for most all wildlife. By the latter part of February, many mule deer were in poor condition. Body weight appeared down and they seemed to lack the vigor and alertness of normal animals."
- "The mule deer situation remains precarious over the West Unit. The area was found to be uniformly overutilized to the point we are in danger of losing a considerable portion of the palatable forage available that deer are dependent upon."
- Data obtained during the winter indicates our doe-fawn ratio to be about 65 fawns per 100 does which is an indication the productivity of the herd has already degenerated to a serious point."
- "An early spring with abundant new growth of forage." (May-Aug.)
- "The limited use of the 1080 baits by coyotes last winter [less than 5% eaten] should indicate that the population is relatively low. However, almost any night these animals can be heard singing at any location along the river".
- "Both cottontails and white-tailed jackrabbits are present in larger numbers. Increased road kills and more sight records seem to support this theory."
- "Body condition [of mule deer] was excellent and during the early part of the hunting season all animals had a wide layer of fat coating the body cavity and internal organs."

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